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Long-term effects of yearly grazing by moulting Greylag geese (*Anser anser*) on reed (*Phragmites australis*) growth and nutrient dynamics

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Abstract

In this study, the effects were quantified of grazing by moulting Greylag geese in spring on biomass and nutrient dynamics of monospecific stands of *Phragmites australis*. A comparison was made between a marsh which had been grazed for more than 15 years, and a site which had not been grazed for at least that period. Both marshes bordered the same lake.

Net above-ground primary production (NAPP) and N and P allocation to above-ground parts were estimated for two growing seasons from regular measurements of the standing shoot biomass and its N and P content, and by using temporary enclosures during goose grazing. Annual NAPP was similar between grazed and ungrazed areas (1997) or higher in the grazed area (1999). Rhizome biomass was similar between areas but the timing of minimum biomass shifted from June to September with grazing. A higher spring shoot emergence due to lower standing dead mass in the grazed area and relocation of reserves from rhizomes to shoots were important in sustaining/increasing NAPP with grazing.

Grazing by moulting Greylag geese in spring approximately doubled the annual allocation of N and P to shoots, and almost tripled the annual above-ground losses of these elements compared to an ungrazed reed vegetation. In the grazed area, 50% or more of the annual nutrient losses were due to goose activity, as no nutrients were resorbed from the nutrient-rich tissue that was consumed or torn and rejected. Differences in timing of shoot emergence in spring were important in affecting the extent of nutrient loss due to goose activity. The increased N and P losses as a result of grazing were associated with consistently lower N and P concentrations in the rhizomes, but only in 1999 were nutrient reserves in rhizomes over winter lower in the grazed reed stand. Resorption efficiency from senescent tissue was increased with grazing in 1997 but not affected in 1999.

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Our results indicate that grazing increased growth and nutrient dynamics of *P. australis* in this eutrophic reed marsh.

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1. Introduction

The effects of herbivory on plant biomass production and nutrient dynamics have been studied at a range of scales, varying from pot experiments to large exclosures in field situations. Multi-year field experiments with exclosures and cutting regimes have shown a wide range of long-term responses to grazing (e.g. Pastor et al., 1993; Gauthier et al., 1995; Ritchie et al., 1998; Schuman et al., 1999; Raillard and Svoboda, 1999; Sirotnak and Huntley, 2000). Such experiments do not only incorporate the effects of biomass removal, but also include the effects of changes in competitive interactions between different plant species (Ritchie et al., 1998; Sirotnak and Huntley, 2000). Several studies have shown that preferential foraging, but also cutting, can have a strong effect on competitive interactions (Furbish and Albano, 1994; Mulder and Ruess, 1998; Van der Wal et al., 2000). Grazing effects on interspecific competition experienced by individual plants may strongly influence their response to grazing in a natural environment, and where more than one species is present, these effects cannot be separated from direct long-term effects of repeated biomass removal (Pastor and Cohen, 1997; Mulder and Ruess, 1998). At the level of individual species, pot and container experiments have identified important interactions between the effects of biomass removal and factors such as nutrients (Ruess, 1984; Chapin and McNaughton, 1989; Hamilton et al., 1998; Hicks and Turkington, 2000), water (Georgiadis et al., 1989; Oosterheld and McNaughton, 1991b) or light (Lentz and Cippolini, 1998). However, the duration of these experiments is usually not longer than one growing season, while the occurrence of compensatory growth has been shown to depend on the time passed since the removal of biomass (Oosterheld and McNaughton, 1991a). It remains difficult to extend these results to field situations.

Monospecific stands of common reed (*Phragmites australis*), a perennial, rhizomatous emergent macrophyte, are commonly found in eutrophic and flooded wetlands. The reed marshes of the Oostvaardersplassen (The Netherlands) have been grazed annually for about 6 weeks in spring by moulting Greylag geese (*Anser anser*) since the beginning of the 1970s (Jans and Drost, 1995). Due to the presence of predators (mainly foxes) the geese have avoided areas with easy access to the drier parts of this nature reserve. Both grazed and ungrazed parts of the marsh are exclusively dominated by *P. australis*.

In the Oostvaardersplassen, we studied the long-term impacts of grazing on plant growth and nutrient dynamics at the plant population level, independently of changes in species composition. Our specific research questions were whether and how yearly grazing influenced primary production, biomass and nutrient dynamics of *P. australis*.

In order to answer these questions, we compared net annual above-ground production (NAPP), rhizome biomass and nutrient dynamics of long-term grazed and ungrazed reed stands over two growing seasons. Thus, in order to accurately identify the effects of

long-term grazing our study relies heavily upon the assumption that initial site differences were negligible compared to effects of grazing. Maps of the area before the colonization by geese did not indicate any difference between the areas in vegetation or soil height, and 2-year enclosure studies gave further evidence that differences could be attributed to annual goose grazing (Jans and Drost, 1995; Van den Wyngaert, 2001).

We used the mass-balance approach to estimate the different types of losses caused by herbivores and senescence of tissues. In view of the many years that the study area had been periodically grazed, we expected a difference in growth between the previously grazed and the ungrazed reed before the geese arrival in May. Taking into account that *P. australis* possesses most of the traits that Belsky et al. (1993) named as favoring vigorous regrowth (i.e. ungrazed storage organs, dormant buds or meristems, ability for fast reallocation of resources, ability for increased photosynthetic rate and ability to use new photosynthates for recovery), it was predicted that grazing would have no effect on NAPP nor on rhizome mass at the start of winter. Considering the eutrophic conditions in this area, we further hypothesized that grazing would increase absolute above-ground nutrient allocation and nutrient losses from the grazed reed vegetation (Ritchie et al., 1998). Since the senescent tissue at the end of the growing season is, on average, younger in grazed reed vegetation, it was predicted that senesced litter would have a higher nutrient concentrations in the grazed than in the ungrazed reed vegetation (Ritchie et al., 1998). We expected that the regrowth of shoots after grazing would draw on the reserves in the storage organs, which in reed are the rhizomes (e.g. Granéli et al., 1992). We expected this to result in a more dynamic pattern (larger differences between minimum and maximum) of rhizome nutrient and biomass dynamics over the year in the grazed reed compared with the ungrazed state.

2. Materials and methods

2.1. Site description

The Oostvaardersplassen (52°26'N, 5°19'E) wetland area has developed since the reclamation of the polder South-Flevoland in lake IJsselmeer, The Netherlands, in 1968. The sediment is former marine clay and eutrophic shallow lakes with extensive reed marshes (3600 ha) have developed, dominated by *P. australis*.

Beginning in the 1970s, Greylag geese have been moulting every year in the area for 6 weeks from about mid May (Zijlstra et al., 1991). Their numbers have increased steadily to approximately 60,000 in 1992 and have from then on decreased till about 15,000 in 1996 (Van Eerden et al., 1997; Bijlsma et al., 2001). In 1997 and 1998 about 26,500 geese came to moult their wing feathers in the marshes of the Oostvaardersplassen (Bijlsma et al., 2001). When foraging, the geese break the reed stems and eat the leave blades and shoot tops, discarding the detached stem parts and leaf sheaths. The geese remain in the marsh until the end of June or early July and, in addition, eat the young regrowth of *Phragmites*. After they depart, *Phragmites* regrows and completes its annual growth cycle (Loonen et al., 1991). Since the geese are unable to fly during the moulting period, their droppings are deposited at the foraging grounds. Most of the nutrient export is in enhanced geese biomass, a value that is small compared to the amount that remains in uneaten plant parts and droppings. About

20% (300 ha) of the marsh area is grazed each year, and the geese return every year to the same part of the marsh (Zijlstra et al., 1991; Jans and Drost, 1995). Grazed areas are now characterized by tussocks of *P. australis* surrounded with standing water in which there is only very sparse shoot growth. Two sites, one in a grazed and one in an ungrazed area, were selected in the eastern part of the Oostvaardersplassen (Krenthoekplas). The grazed site was selected in an area where grazing had started between 1974 and 1985. The ungrazed site was chosen in an area which had probably never been grazed (Jans and Drost, 1995). Both sites were flooded in winter. In the ungrazed site accumulation of organic material has resulted in an increase in the sediment surface compared to the grazed site. The water table drops below the sediment surface in early to late summer in the ungrazed site in most years, and rises again in autumn and winter, depending on annual rainfall. In the grazed site less accumulation of organic matter has taken place, and this site is flooded at least till July.

2.2. Experimental design

In the grazed and ungrazed sites, the dynamics of above-ground biomass, rhizome mass and plant nutrient concentrations were measured during 2 years in randomly selected replicate plots (more than 30 m apart), used as permanent plots within one growing season ($n = 10$ in 1997; $n = 6$ in 1999). Regrowth and consumption, which occurred simultaneously during the presence of the geese, was estimated using temporary enclosures constructed each within 3 m of a replicate plot of the respective year ($n = 10$ in 1997; $n = 6$ in 1999).

2.3. Sampling methods

The above-ground biomass of *P. australis* was estimated for each plot in a $1\text{ m} \times 1\text{ m}$ sampling quadrat at 3–6 weeks intervals between March and October 1997 and between March and November 1999. In all plots living and dead shoots were counted, and 15 living shoots and 15 dead stems were collected randomly within 2 m of the sampling quadrat. The shoots were cleaned with tap water if necessary, dried at 70°C for at least 48 h and weighed. At the sampling in May and on the 1st of October (1997) and 15th of September (1999), the shoots were separated into stem (including leaf sheath) and leaf blade material before drying. On all other sampling dates intact shoots were dried.

In June 1998 and 1999, a number of tussocks (diameter approx. 0.8 m) were enclosed after grazing using temporary enclosures, which prevented the geese from consuming regrowing plants. The number of stems in each enclosure was counted at the start and at the end of a 3-week interval, after which the regrowth material was harvested, dried and weighed. Mean regrowth rate per day was calculated to estimate total regrowth during the grazing period (4 weeks of regrowth was assumed and extrapolated from data based on 3 weeks).

The density of living shoots per plot was multiplied by average weight of living shoots to calculate standing biomass. Annual net above-ground primary production (NAPP) was then calculated as the sum of maximal biomass increase over the year and the biomass of shoots that have died over the year (Mason and Bryant, 1975). For the grazed site, production was estimated by adding the maximal biomass increase before grazing to the maximal biomass increase during and after grazing, that included regrowth of shoots. The biomass which

senesced at the end of the season was estimated as the difference between NAPP and the amount removed by geese.

Rhizomes were sampled in March, June, September and November 1997 and in March and June 1998, and again in November 1999. Cores, diameter of 16.2 cm and length of 75 cm, were taken at each of the grazed and ungrazed locations that were used for above-ground sampling, between 2 and 5 m from each plot. In the ungrazed site, only one core was taken per plot, while in the grazed site, one core was taken in the middle of a tussock, and another between tussocks.

Mud was removed as much as possible from the samples in the field, after which they were taken to the laboratory and stored at -20°C . Living and dead rhizome material was separated after washing using color, smell and rigidity as indicators, and roots and other organic material removed. Rhizome material was dried at 70°C for at least 48 h.

For the grazed site, biomass per surface area was calculated as the weighed average of the biomass between and in tussocks. The relative area covered by tussocks was measured in May 1997 by mapping the tussocks in the grazed site and calculating their surface area. The basal cover of the tussocks occupied 35% of the total area.

2.4. *Nutrient concentrations, uptake and resorption from dying tissue*

The dried plant material was ground using a centrifugal mill and digested using an adaptation of the Kjeldahl method (Bremner and Mulvaney, 1982). The nitrogen (N) and phosphorus (P) concentrations of the diluted supernatant were determined colorimetrically using a continuous-flow autoanalyzer (Skalar SA-40, The Netherlands).

The total net above-ground allocation of N and P was estimated as the sum of the maximal standing amounts of N and P and the amount of these nutrients in shoots that were removed by the geese in grazed plots. In ungrazed plots, the maximal levels of standing N and P were used as an estimate of net allocation.

In November 1997 and 1999, the N and P concentrations of current season's standing dead leaves and stems were determined for both areas. In 1997, plant material was collected outside the plots, while in 1999 these data were obtained at the last sampling date in the plots. Estimated resorption of N and P from senescing above-ground material to rhizomes was calculated by subtracting amounts of these elements removed by geese, the amount of N and P in dead material and the amount of these elements in seeds (data only available for 1999) from total net annual above-ground accumulation of N and P.

2.5. *Statistical analysis*

All variables were analyzed using a repeated measures analysis of variance (ANOVA), with year and grazing treatment as between-subject factors and time as a within-subject factor. Data were tested for normality and homogeneity of variance, and all biomass data were log-transformed before analyses to meet these requirements. If the requirements of sphericity were not met for the repeated measures analysis, Greenhouse–Geisser adjusted mean squares and *P*-values were used. This altered the outcome of the ANOVA tests for none of the variables. In case of significant interactions between main effects, relevant contrasts were then examined per sampling date using analysis of variance, or individually

using paired (differences in time within one site) or unpaired (differences between years or sites) Student’s *t*-tests. All analyses were performed using SPSS 8.0 for Windows (SPSS, Chicago, Illinois, USA).

3. Results

3.1. Impact of grazing on shoot and rhizome biomass

Repeated measures analysis of above-ground biomass for site (grazed versus ungrazed) and year (1997 versus 1999) over the season showed a significant three-way interaction, therefore a two-way analysis of variance was performed for each month separately (Table 1). The effect of grazing on the biomass of *P. australis* was significant only for the period May–July, i.e. just before and during the presence of the geese (Fig. 1A, Table 1). In May of both years, living shoot mass was a factor 2.5 (1997) and 1.5 (1999) higher in the grazed site than in the ungrazed site. Consumption by the grazing geese of about 70% of the shoot biomass decreased this amount to approximately 150–200 g m⁻² in both the years, which was similar to the amount of biomass in the ungrazed site in June 1997, but significantly lower than the ungrazed reed biomass in June 1999. In July of both years, the biomass of the grazed reed was lower than that of the ungrazed reed, but this was only significant in 1997. In August and September, the grazed site had consistently lower biomass, but the differences were not statistically significant (Table 1). Maximum standing biomass was reached in September and ranged between an estimated 700 and 1050 g m⁻².

Emergence was somewhat later in 1999 compared with 1997, as indicated by a significantly lower biomass in March (Fig. 1A), and biomass increased faster, as shown by a significantly higher biomass in May. However, these differences between years disappeared

Table 1
Results of two-way ANOVAs for each measuring date of above-ground biomass and rhizome biomass with site and year as main effects

	Site		Year		Site × year	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Above-ground biomass						
March	3.946	0.057	32.539	<0.001	1.545	0.224
May	31.794	<0.001	11.421	0.002	3.681	0.065
June	14.073	0.001	5.913	0.022	15.225	0.001
July	52.957	<0.001	5.718	0.024	5.332	0.029
August	5.521	0.028	0.932	0.344	0.262	0.613
September	2.730	0.110	3.625	0.067	0.590	0.449
Rhizome mass over winter (November)						
Live	1.667	0.207	1.358	0.254	1.868	0.183
Dead	10.613	0.003	3.949	0.057	0.249	0.622

The critical *P*-value is corrected using Bonferroni (*P* < 0.008 (=0.05/6)). Significant main effects are shown in bold only when the interaction term is not significant (*P* < 0.05).

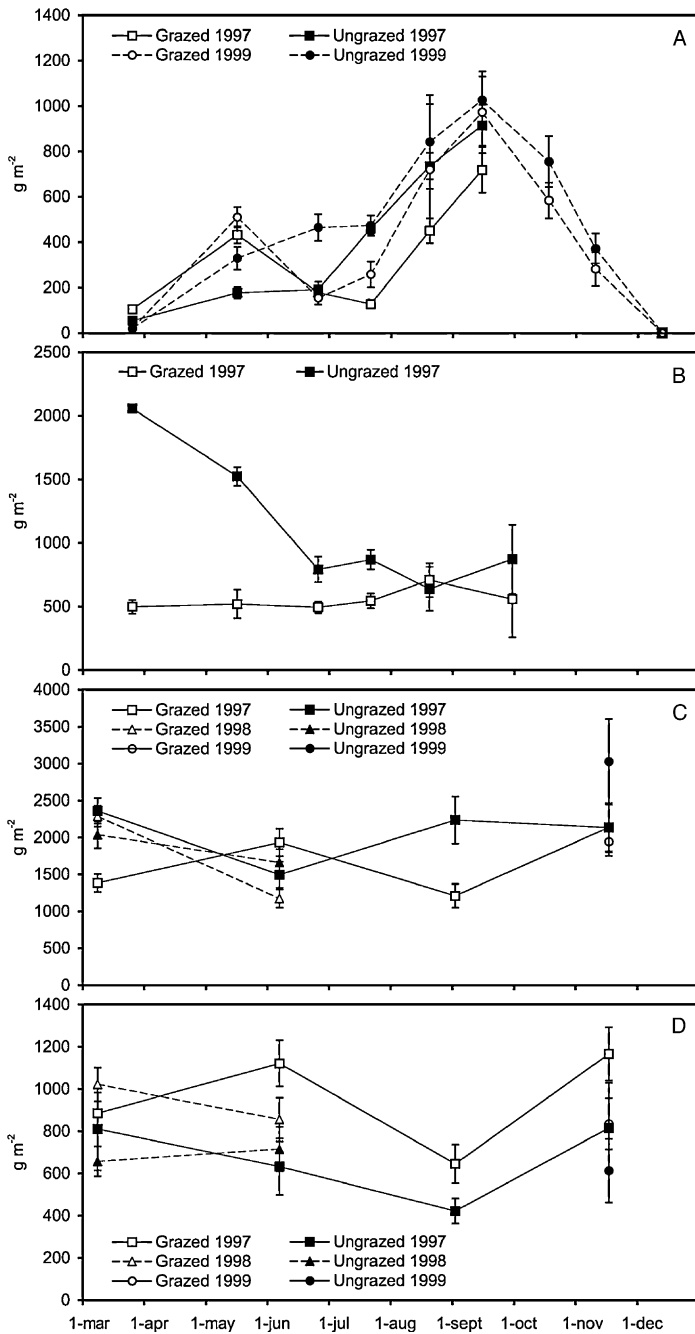


Fig. 1. Living (A) and dead (B) shoot mass and living (C) and dead (D) rhizome mass in the grazed (open symbols) and ungrazed (filled symbols) reed vegetation in 1997, 1998 (for rhizomes only) and 1999.

Table 2

Repeated measures analysis of living and dead rhizome mass and rhizome nutrient concentrations

	Site			Time of season			Site × time of season		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Live rhizomes									
Mass	1	4.390	0.051	5	4.314	0.008	5	5.310	0.003
N concentration	1	34.799	<0.001	5	13.274	<0.001	5	0.726	0.548
P concentration	1	14.869	0.001	5	6.977	<0.001	5	0.437	0.768
Dead rhizomes									
Mass	1	8.295	0.010	5	4.145	0.007	5	1.077	0.371

Significant main effects are shown in bold only when the interaction term is not significant ($P < 0.05$).

during the course of the growing season and were not significant from August onwards (Fig. 1A, Table 1). Only in June and July a significant interaction between site and year effects was found (Table 1). Pairwise comparisons showed that at the ungrazed site biomass differed significantly between years in June, while at the grazed site there was only a significant year effect in July ($P < 0.05$). Biomass increase in spring was slower in the ungrazed reed, especially in 1997 (Fig. 1A).

Standing dead material was significantly higher for the ungrazed reed in March and May 1997 ($P < 0.05$) and decreased rapidly from approximately 2000 g m^{-2} in March to about 800 g m^{-2} in June (Fig. 1B). At this time, standing dead material at both sites did not differ ($P < 0.05$). In 1997, living biomass in the ungrazed area started to increase rapidly only between June and July, i.e. after the standing dead mass had decreased substantially.

Living rhizome biomass ranged between an estimated 1200 and 2400 g m^{-2} between March 1997 and June 1998 (Fig. 1C). Repeated measures analysis showed a significant interaction between the effects of grazing and time (Table 2). Significant differences between the sites were found only in March and September 1997, and in both cases the ungrazed reed had significantly higher rhizome biomass than the grazed reed. Rhizome sampling in 1999 was in different replicate plots than those in 1997–1998, and results could therefore not be analyzed with a repeated measures analysis. Two-way ANOVA analysis of rhizome biomass in November 1997 and 1999 showed neither a significant effect of grazing, nor a significant difference between years (Table 1). Rhizome biomass dynamics over the year were mostly not significant due to the large variances and statistical restrictions reducing the power of the tests. In the ungrazed vegetation, rhizome biomass tended to decrease between March and June, and increase again between June and November (Fig. 1C). In the grazed vegetation, rhizome biomass decreased significantly between June and September and significantly increased in biomass between September and November. In both areas, the estimated biomass of living rhizomes did not change over winter.

The reed in the grazed site had 10–80% more dead rhizome mass than the reed in the ungrazed area (Fig. 1D, Table 2). Dead rhizome mass decreased significantly in summer and increased significantly in autumn in both areas. There was no interaction between the effects of time and grazing on the amount of dead rhizome mass (Table 2).

3.2. Effects of grazing on nutrient dynamics

A significant three-way interaction between the effects of site, year and sampling date, was found for N and P concentrations as well as N and P amounts in above-ground material. N and P concentrations were either similar or higher in 1997 than in 1999, with differences ranging from 1 to 40% (Table 3). The concentrations of these elements did not differ between reed from grazed and ungrazed sites, except in June, shortly after the geese had selectively removed the most nutrient-rich parts of shoots (Table 3). In November 1999, i.e. during senescence, N concentrations of remaining living shoot mass tended to be higher, and P concentrations were significantly higher in the grazed reed vegetation compared with the ungrazed reed.

Table 3

N and P concentrations of above-ground biomass over the growing season, and analysis of variance of N and P concentrations of above-ground biomass with site and year as main effects

	1997		1999		Site	Year	Site × year
	Grazed	Ungrazed	Grazed	Ungrazed			
N concentration (mg g ⁻¹)							
March	30.2 ± 0.7	29.4 ± 0.7	23.0 ± 0.8	28.8 ± 1.0	0.002	<0.001	<0.001
May	23.1 ± 0.7	25.0 ± 0.5	20.0 ± 0.9	19.9 ± 0.8	NS	<0.001	NS
June	12.2 ± 0.5	27.8 ± 0.5	12.6 ± 1.0	19.4 ± 1.9	<0.001	0.039	>0.001
July	20.5 ± 0.6	24.4 ± 0.7	20.0 ± 2.3	19.6 ± 1.6	NS	0.021	NS
August	19.7 ± 0.8	17.2 ± 0.4	15.4 ± 1.4	16.5 ± 0.8	NS	0.005	0.039
September	17.1 ± 0.7	14.9 ± 0.5	15.3 ± 1.0	14.5 ± 0.7	0.030	NS	NS
October			13.1 ± 0.8	11.9 ± 0.2	NS		
November			11.3 ± 0.9	9.0 ± 0.3	0.024		
P concentration (mg g ⁻¹)							
March	3.43 ± 0.04	3.60 ± 0.10	2.83 ± 0.10	3.53 ± 0.14	<0.001	0.001	0.005
May	3.02 ± 0.08	3.19 ± 0.08	2.35 ± 0.09	2.50 ± 0.13	NS	>0.001	NS
June	1.65 ± 0.04	3.00 ± 0.05	1.54 ± 0.11	2.11 ± 0.20	<0.001	<0.001	<0.001
July	2.31 ± 0.06	2.51 ± 0.05	2.40 ± 0.25	1.85 ± 0.13	NS	0.018	0.003
August	2.07 ± 0.08	1.80 ± 0.09	1.47 ± 0.17	1.47 ± 0.10	NS	>0.001	NS
September	1.32 ± 0.07	1.14 ± 0.05	1.28 ± 0.05	1.21 ± 0.07	NS	NS	NS
October			0.85 ± 0.06	0.85 ± 0.03	NS		
November			0.72 ± 0.06	0.53 ± 0.03	0.012		
N:P ratio							
March	8.8 ± 0.2	8.2 ± 0.2	8.1 ± 0.1	8.1 ± 0.2	NS	NS	NS
May	7.6 ± 0.2	7.9 ± 0.2	8.5 ± 0.2	8.0 ± 0.3	NS	0.011	NS
June	7.4 ± 0.3	9.3 ± 0.5	8.3 ± 0.5	9.2 ± 0.3	<0.001	NS	NS
July	8.9 ± 0.3	9.8 ± 0.5	8.4 ± 0.5	10.6 ± 0.4	<0.001	NS	NS
August	9.6 ± 0.4	9.7 ± 0.4	10.7 ± 0.8	11.3 ± 0.5	NS	0.012	NS
September	13.1 ± 0.5	13.1 ± 0.4	11.9 ± 0.3	12.1 ± 0.5	NS	0.027	NS
October			15.5 ± 0.4	14.1 ± 0.4	NS		
November			15.7 ± 0.7	17.2 ± 1.2	NS		

The critical *P*-value is corrected using Bonferroni ($P < 0.008 (=0.05/6)$). Significant main effects are shown in bold and given only when the interaction term is not significant ($P < 0.05$).

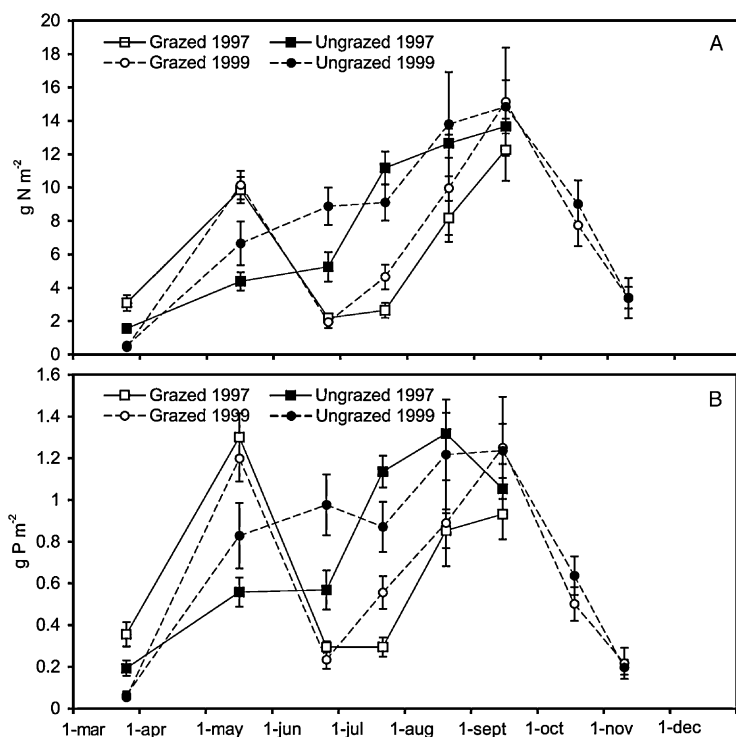


Fig. 2. N (A) and P (B) content of shoot mass in the grazed (open symbols) and ungrazed (filled symbols) reed vegetation in 1997 and 1999.

The grazed and ungrazed reed had similar N:P ratios, except for small but significant differences in June and July of both years, when N:P ratios of shoots were significantly lower in the grazed area (Table 3). The N:P ratios increased significantly over the growing season and further increased significantly during senescence from September to November.

As the differences in N and P concentrations between sites were small or absent, with June as an obvious exception, the effects of grazing (site effects) on both N and P standing mass clearly reflected the differences in biomass dynamics between sites (Fig. 2A and B). In May 1997, above-ground N and P mass was significantly higher in the grazed sites than in the ungrazed sites (Table 4). Similar to the results found for biomass, there was a significant interaction between site and year effects in June and July (Table 4). This was due mainly to the higher N and P mass in June 1999 compared to 1997 in the ungrazed reed vegetation, and a more rapid recovery of the above-ground mass and its N and P content after grazing of reed in July 1999. N and P mass in the grazed reed vegetation dropped in both the years to about 22% of the amounts present before goose grazing.

N and P concentrations of the rhizomes were consistently and significantly lower (about 30% for N and about 20% for P) in the grazed than in the ungrazed site (Table 5, see Tables 2 and 4 for statistics). Rhizome nutrient concentrations in November were similar between 1997 and 1999 (Table 4). Between March 1997 and June 1998, nutrient concentrations

Table 4

Results of two-way ANOVAs for each measuring date of above-ground nutrient mass (g m^{-2}) and rhizome nutrient mass (g m^{-2}) with site and year as main effects

	Site		Year		Site \times year	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Above-ground N mass						
March	2.647	0.115	43.190	>0.001	3.403	0.076
May	31.136	<0.001	3.869	0.059	2.662	0.114
June	58.253	<0.001	1.627	0.213	6.309	0.018
July	64.126	<0.001	2.230	0.147	8.827	0.006
August	7.468	0.012	0.100	0.754	0.018	0.895
September	0.512	0.480	1.286	0.266	0.113	0.739
Above-ground P mass						
March	3.072	0.091	29.724	>0.001	4.149	0.051
May	29.824	<0.001	1.155	0.292	3.403	0.076
June	64.277	<0.001	3.855	0.060	9.038	0.006
July	67.169	<0.001	0.318	0.578	14.690	0.001
August	8.053	0.010	0.159	0.694	0.175	0.680
September	0.317	0.578	3.365	0.077	0.172	0.682
Rhizome nutrients over winter (November)						
N concentration	17.402	<0.001	1.212	0.280	1.925	0.176
N mass	8.473	0.007	1.942	0.174	4.259	0.048
P concentration	10.481	0.003	0.222	0.641	0.790	0.382
P mass	8.280	0.008	1.326	0.259	2.274	0.143

The critical *P*-value is corrected using Bonferroni ($P < 0.008 (=0.05/6)$). Significant main effects are shown in bold only when the interaction term is not significant ($P < 0.05$).

Table 5

N and P concentrations (mg g^{-1}) and mass (g m^{-2}) of rhizomes over time (mean \pm S.E.) between March 1997 and November 1999 in the grazed (G) and ungrazed (U) area

	March 1997	June 1997	September 1997	November 1997	March 1998	June 1998	November 1999
N concentration (mg g^{-1})							
G	7.8 \pm 0.3	7.3 \pm 0.4	5.6 \pm 0.4	7.1 \pm 0.7	7.8 \pm 0.3	6.4 \pm 0.4	6.9 \pm 0.5
U	10.0 \pm 0.7	10.2 \pm 0.5	7.5 \pm 0.3	8.6 \pm 0.2	10.3 \pm 0.4	8.7 \pm 0.4	10.0 \pm 0.7
P concentration (mg g^{-1})							
G	1.32 \pm 0.06	1.17 \pm 0.08	0.95 \pm 0.09	1.09 \pm 0.12	1.31 \pm 0.11	1.22 \pm 0.11	1.04 \pm 0.14
U	1.60 \pm 0.08	1.37 \pm 0.08	1.25 \pm 0.07	1.35 \pm 0.04	1.53 \pm 0.07	1.54 \pm 0.11	1.51 \pm 0.16
N:P ratio							
G	5.9 \pm 0.2	6.4 \pm 0.4	6.1 \pm 0.3	6.6 \pm 0.2	6.7 \pm 0.3	5.8 \pm 0.2	6.9 \pm 0.9
U	6.2 \pm 0.1	7.5 \pm 0.1	6.1 \pm 0.1	6.4 \pm 0.1	6.2 \pm 0.1	5.3 \pm 0.1	7.0 \pm 0.8
N mass (g m^{-2})							
G	10.9 \pm 1.2	14.1 \pm 1.3	6.5 \pm 0.8	15.5 \pm 3.5	17.7 \pm 1.2	7.3 \pm 0.7	13.3 \pm 1.4
U	23.0 \pm 1.8	13.8 \pm 1.3	16.0 \pm 2.0	18.3 \pm 2.5	21.0 \pm 2.0	14.2 \pm 1.5	29.7 \pm 4.4
P mass (g m^{-2})							
G	1.82 \pm 0.18	2.33 \pm 0.30	1.08 \pm 0.13	2.35 \pm 0.53	2.97 \pm 0.27	1.41 \pm 0.14	2.05 \pm 0.94
U	3.72 \pm 0.26	1.89 \pm 0.22	2.79 \pm 0.40	2.88 \pm 0.42	3.13 \pm 0.29	2.52 \pm 0.29	4.50 \pm 0.84

of both the grazed and ungrazed vegetation showed a significant decrease from March to September, followed by a significant increase in autumn and winter ($P < 0.05$) (Table 5). The N:P ratio of the rhizomes ranged between 5.5 and 7.5 over the season, but did not show a consistent pattern (Table 5).

Differences in nutrient concentrations were rather small compared with the differences in rhizome biomass, therefore dynamics and patterns of N and P mass in rhizomes followed closely those of rhizome biomass. Pairwise comparisons revealed significantly higher N and P masses in the ungrazed site for March and September 1997, June 1998 and November 1999 (Table 5).

3.3. Consequences of the effects of grazing on NAPP and cycling of N and P over the growing season

Whereas net above-ground primary production (NAPP) was not significantly different between grazed and ungrazed reed in 1997, in 1999 the NAPP of the grazed reed vegetation was significantly ($P < 0.05$) higher (about 50%) than that of the ungrazed reed ('a' in Table 6). NAPP was not different between years for the ungrazed site, but was significantly higher in 1999 in the grazed site ($P < 0.05$). In both the years, there was significantly lower production of senescent litter under grazed than under ungrazed conditions ('e' in Table 6). In the ungrazed area all biomass died off and became litter. In contrast, in the grazed area only about 60% of net yearly above-ground production was left to die off at the end of the growth season, and an additional 4% died after the geese had consumed the vegetation ('d' in Table 6). More than 30% (390 g m^{-2} in 1997 and 472 g m^{-2} in 1999) was removed by goose activity. Of these amounts, about 60%, i.e. 230 g m^{-2} in 1997 and 306 g m^{-2} in 1999, had been consumed ('b' in Table 6). The rest were broken stem parts that had been discarded by the geese ('c' in Table 6). However, the total input of organic material into the water and sediment over the whole year equaled NAPP, and thus was similar between the grazed and ungrazed site in 1997 and higher in the grazed site in 1999 ('h' in Table 6).

Above-ground N and P allocation was similar between years, and above-ground accumulation of these elements in the grazed *P. australis* vegetation was consistently and significantly higher than in the ungrazed site ('a' in Table 6). Between 50 and 95% of above-ground total N and P allocation over the growing season was lost from the plant, either due to grazing, or through litter production in autumn. Consumption, spilling of discarded material by grazing geese and shoot death after grazing, i.e. geese-related pathways, contained $10\text{--}15 \text{ g N m}^{-2}$, i.e. approximately 50% of annual above-ground allocation of N, and $1.4\text{--}1.6 \text{ g P m}^{-2}$, i.e. approximately 60% of annual above-ground allocation for P ('b', 'c', and 'd' in Table 6). These geese-related pathways accounted for between 50 and 85% of total annual losses of these nutrients from the grazed vegetation.

Nitrogen and phosphorus losses associated with senescence in autumn were lower in the grazed than in the ungrazed reed vegetation, and higher in 1999 than in 1997 ('e' in Table 6). For P, the effect of grazing was significant in 1997 only. Still, on an annual basis, the reed vegetation in the grazed site lost about twice as much N and between two and three times as much P as the reed vegetation in the ungrazed site ('h' in Table 6).

In both the years, the amount of N relocated from dying tissue to the storage organs was higher in grazed than in ungrazed reed, while the amount of P relocated did not differ between

Table 6
Annual above-ground biomass and nutrient dynamics of the grazed and ungrazed *Phragmites australis* vegetation [mean \pm S.E. (% of NAPP response annual above-ground N or P allocation)] and analysis of variance of annual above-ground biomass and nutrient dynamics with site and year as main effects

	1997		1999		Site × year	Year	Site
	Ungrazed reed	Grazed reed	Ungrazed reed	Grazed reed			
Biomass							
(a)	1100 ± 25 (100)	1145 ± 35 (100)	1025 ± 104 (100)	1511 ± 145 (100)	0.031	NS	0.013
(b)		230 ± 3 (20)		306 ± 25 (20)		0.002	
(c)		160 ± 7 (14)		166 ± 39 (11)		NS	
(d)		37 ± 3 (3)		67 ± 28 (4)		NS	
(e)	1100 ± 25 (100)	718 ± 33 (63)	1025 ± 104 (100)	972 ± 180 (64)	NS	NS	0.013
(h)	1100 ± 25 (100)	1145 ± 35 (100)	1025 ± 104 (100)	1511 ± 145 (100)	0.031	NS	0.013
Nitrogen							
(a)	13.7 ± 0.5 (100)	23.8 ± 0.6 (100)	14.8 ± 1.6 (100)	29.2 ± 2.9 (100)	NS	NS	< 0.001
(b)		8.2 ± 0.1 (35)		9.2 ± 0.6 (32)		NS	
(c)		2.8 ± 0.2 (12)		4.7 ± 0.8 (16)		NS	
(d)		0.4 ± 0.0 (2)		0.3 ± 0.1 (1)		NS	
(e)	9.5 ± 0.2 (70)	5.4 ± 0.2 (23)	12.3 ± 1.9 (83)	10.6 ± 2.3 (36)	NS	0.001	0.002
(f)	4.1 ± 0.3 (30)	6.9 ± 0.4 (30)	1.8 ± 1.0 (12)	3.8 ± 1.4 (13)	NS	< 0.001	0.041
(g)			0.7 ± 0.2 (5)	0.5 ± 0.2 (2)			NS
(h)	9.5 ± 0.2 (70)	16.9 ± 0.3 (70)	13.0 ± 2.0 (95)	25.4 ± 2.2 (87)	NS	< 0.001	< 0.001
Phosphorus							
(a)	1.32 ± 0.03 (100)	2.36 ± 0.04 (100)	1.24 ± 0.13 (100)	2.65 ± 0.26 (100)	NS	NS	< 0.001
(b)		0.84 ± 0.01 (36)		0.79 ± 0.05 (30)		NS	
(c)		0.52 ± 0.02 (22)		0.73 ± 0.09 (28)		NS	
(d)		0.06 ± 0.00 (3)				NS	
(e)	0.61 ± 0.01 (47)	0.23 ± 0.01 (10)			0.003	0.001	<0.001
(f)	0.70 ± 0.02 (53)	0.69 ± 0.03 (29)			NS	0.001	NS
(g)						NS	
(h)	0.61 ± 0.01 (47)	1.67 ± 0.03 (71)			NS	0.001	<0.001

Significant main effects are shown in bold and given only when the interaction term is not significant ($P < 0.05$). (a) Annual net above-ground accumulation (NAPP), (b) loss of mass consumed by geese, (c) loss of mass spilled by geese, (d) loss of mass through die-off after geese grazing, (e) litter production through senescence at the end of the growing season, (f) reallocation to rhizomes, (g) nutrient export through seeds (available for 1999 only), (h) total annual losses.

Table 7

N and P concentrations (mg g^{-1}) of dead shoot material in November and N and P resorption efficiencies (%) from senescing shoot material (mean \pm S.E.)

	1997		1999	
	Grazed	Ungrazed	Grazed	Ungrazed
N concentration	7.5 ± 0.2^a	8.7 ± 0.3^a	10.9 ± 1.2 a	11.9 ± 0.9 a
N resorption (%)	56 ± 2 a	28 ± 4 b	24 ± 7 a	13 ± 7 a
P concentration	0.33 ± 0.02^a	0.56 ± 0.4^a	0.65 ± 0.10 a	0.68 ± 0.09 a
P resorption (%)	74 ± 2 a	52 ± 2 b	37 ± 7 a	37 ± 9 a

Different letters signify significant differences between grazed and ungrazed sites at the $P < 0.05$ level.

^a Calculated values.

sites ('f' in Table 6). However, resorption efficiencies of both N and P were significantly higher in the grazed site in 1997, while in 1999 resorption efficiencies were not significantly different between grazed and ungrazed reed (Table 7).

4. Discussion

This study was designed to quantify the effects of grazing by moulting Greylag geese in spring on biomass and nutrient dynamics of monospecific stands of *P. australis*.

One of the most striking effects of the long grazing history was a much higher biomass production and above-ground standing nutrient content before the end of May in the grazed compared with the ungrazed reed vegetation. This provided the geese with a greater amount of food, be it with equal N concentration, than that which was available in the site which had never been grazed. Repeated grazing by herbivores has often been found to increase either food quantity or quality or both (Ydenberg and Prins, 1981; Hik et al., 1992; Fox et al., 1998; Rowcliffe et al., 1998; Mayhew and Houston, 1999). This can occur through various mechanisms, e.g. ranging from changes in species composition (Rowcliffe et al., 1998) or the delay of succession (Hik et al., 1992), increased cycling of limiting nutrients (Cargill and Jefferies, 1984; Hik et al., 1991) or simply rejuvenation of tissue (Fox et al., 1998; Mayhew and Houston, 1999). None of these mechanisms operated in early May in the *P. australis* stands considered in this study. The increased net above-ground production so early in the season could have resulted from a higher availability of carbohydrates and nutrients in the storage organs in grazed conditions. In March, just before emergence, rhizome biomass and N and P content were higher in the grazed site, but these differences were small and unlikely to have such a large stimulating effect on emergence.

More likely the difference in above-ground primary production between the grazed and ungrazed site was an effect of the large difference in standing dead mass during this period in spring (Fig. 1B). In the ungrazed site, standing dead mass decreased strongly in spring and early summer, probably as stems broke and became part of the litter layer. This pattern was also found by Mason and Bryant (1975) in their study of an undisturbed reed marsh. They found no decrease in standing dead shoot mass over winter, but a steady loss of standing dead shoot mass in spring and summer. In contrast, standing dead shoot mass of grazed

reed in 1997 was much lower already in March and hardly decreased over the growing season. Regrown shoots are thinner and break more easily (Van Eerden et al., 1997; Van den Wyngaert, 2001). Therefore, they likely suffer more from winter storms, and less dead shoots remain standing in spring. Lower standing dead mass probably triggered a faster emergence and rate of spring growth in the grazed *P. australis* vegetation, as found after removal of standing old stems in Belgium (Gryseels, 1989), Sweden (Granéli, 1989; Ekstam, 1995) and England (Haslam, 1971). Both shading effects (Ekstam, 1995) and differences in microclimate (Haslam, 1969) may decrease shoot natality in the spring cohort if many standing dead stems are present. Additionally, in spring 1999, there was a heavy infestation of the reed borer (*Archanara geminipuncta*) in the ungrazed reed (Van den Wyngaert, 2001), which may have reduced biomass production. Reed borers need thick stems (Tscharnkte, 1999), which are lacking in the grazed area (Van Eerden et al., 1997), to complete their life cycle, together with standing litter needed for hibernation (Van der Toorn and Mook, 1982). Thus, the delay or reduction in biomass production in spring in the ungrazed reed was associated with higher stem diameters resulting in more standing litter over winter and spring, and this both decreased shoot natality and increased insect damage in the ungrazed reed.

Grazing activities by geese removed 35% of annual NAPP, 50% of annual N and about 60% of annual P allocation to the shoots in only 5–6 weeks (Table 6). This included estimated consumption of regrowth, as measured from temporary exclosures. Despite this drastic effect on canopy biomass and nutrient content, spring grazing by moulting geese did not reduce NAPP and even stimulated it in 1999. Similar neutral or positive responses have been recorded for other wetland grasses and graminoids (Cargill and Jefferies, 1984; Beaulieu et al., 1996; Person et al., 1998; Mulder and Ruess, 1998; Lentz and Cippolini, 1998; Raillard and Svoboda, 1999). Annual nutrient allocation to the reed shoots increased by 60–80% due to grazing and this effect has also been found in several cutting experiments (Raillard and Svoboda, 1999; Mayhew and Houston, 1999). This similar NAPP in the grazed site was reached with only 35% of the sediment surface covered by densely growing tussocks (Van den Wyngaert, 2001), however, the long reed stems were bent outward at the edges of the tussocks and obviously still reached a full canopy cover, efficiently catching incoming radiation.

Several mechanisms have been identified which may cause an increase in productivity of the remaining tissue after biomass removal (see, e.g. Hilbert et al., 1981; Oosterheld, 1992; Belsky et al., 1993) or compensate for increased nutrient losses by increased nutrient uptake (Chapin and Slack, 1979; Thornton and Millard, 1996). *P. australis* has rhizomes that contain reserve carbohydrates and nutrients, dormant buds to replace damaged shoots or shoot parts (Haslam, 1969), and in this eutrophic system plant growth does not seem to be limited by nutrient uptake (low N:P ratios may indicate N limitation as well as no nutrient limitation; Spink et al., 1998; Wassen et al., 1998). Therefore, fast regrowth was expected to occur once the moulting Greylag geese had left the area in July (Belsky et al., 1993). Additionally, grazing occurred early in the season, which in *Phragmites* is important for the replacement of broken shoots (Haslam, 1969). It lasted for a relatively short period of time, and, most importantly, allowed for a long period for recovery, which is favorable for compensation to occur (Oosterheld and McNaughton, 1991a; Oosterheld, 1992). Regrowth was greatest from the end of July till peak standing crop in September. This vigorous

regrowth was at least partly stimulated by relocation of nutrients and probably also carbohydrates from the rhizomes, as regrowth occurred at the expense of below-ground reserves in September. In the ungrazed reed, minimum rhizome biomass occurred in June, similar to results found in Sweden (Granéli et al., 1992), The Netherlands (Van der Linden, 1980) and Czechoslovakia (Fiala, 1976). Thus, grazing shifted the time of minimal reserves in the rhizomes from early to late summer, and increased the difference between minimum and maximum rhizome biomass and amounts of N and P. Depletion of below-ground storage reserves has also been measured as an immediate response to grazing in pot experiments as well as in field measurements (Chapin and Slack, 1979; Oosterheld, 1992; Johansson, 1993; Beaulieu et al., 1996; Thornton and Millard, 1996; Hamilton et al., 1998). However, in our study *P. australis* fully compensated for biomass and nutrient losses through regrowth of rhizome biomass and accumulation of N and P in autumn. Export of nutrients and probably also carbohydrates through seeds was small compared to other losses, and did not account for the large difference in rhizome growth between the areas. Still, a decreased flowering rate in the grazed area (Van den Wyngaert, 2001) may have prolonged vegetative growth and nutrient uptake in autumn and thus have stimulated rhizome growth during that period. Several field studies in a wide range of ecosystems found no negative effect of grazing on below-ground biomass in natural situations (Cargill and Jefferies, 1984; McNaughton et al., 1998; Morris and Jensen, 1998; see also Milchunas and Lauenroth, 1993).

The increase between minimum and maximum rhizome biomass between March 1997 and March 1998 was about 46% higher in the grazed than in the ungrazed reed, suggesting a similar difference in turn over rate. Additionally, dead rhizome mass, averaged for all sampling dates, was 40% higher in the grazed than in the ungrazed site, with no indication of differences in decomposition rates between the sites (Van den Wyngaert, 2001). Considering the large variances in the measurement of rhizome mass, these estimates are remarkably similar. The occurrence of a higher mortality rate, or a higher mass of dead root and rhizome material in the soil, of grazed compared to ungrazed field conditions has been found in other studies as well (Richards, 1984; Morris and Jensen, 1998).

While peak standing nutrient mass was similar between sites, the amounts of N and P contained in senescent litter were lower in reed vegetation that had been grazed. This effect was most pronounced in 1997. In that year, resorption efficiency from senescing tissue was significantly higher in the regrown reed. This agrees with results found by May and Killingbeck (1995) for insect grazing on trees, which was the only other study we have found that compared resorption efficiencies from regrowth and undisturbed plants. In 1997, this resulted in lower litter N and P concentrations for regrown material. This was contrary to our expectations, and refutes the general assumption that younger material necessarily produces better quality litter (e.g. Ritchie et al., 1998; Sirotiak and Huntley, 2000).

In both the years, the resorption efficiency for P was higher than for N (e.g. Bobbink et al., 1989). N:P ratios were lowest in storage organs, higher in emerging shoots and increased over the growing season (Ulrich and Burton, 1985; Dinka, 1986; Granéli, 1990; Romero et al., 1999), except when induced regrowth stimulated nutrient relocation from the relatively P-rich rhizomes in June and July. Similar values and patterns as for the ungrazed reed were found by Van der Linden (1980, 1986) working in a nearby area. Overall, the patterns in 1997 and 1999 were remarkably similar. Most differences between years indicated a faster growth, stronger dilution of nutrients and thus better light conditions in 1999. Indeed,

though both years were sunnier than average, 1999 had a higher overall average temperature and a higher spring temperature, and more hours of sunshine than 1997. These differences seemed especially important for shoot emergence in the ungrazed area, and also increased recovery after grazing, with significant overcompensation only in 1999. The water level, which is managed in this polder-marsh, was lower in 1999 than in 1997. This affected sediment redox potentials to a larger extent in the grazed than in the ungrazed area (Van den Wyngaert, unpublished results). If the relatively low sediment redox potential acted as a stress for reed growth, this stress may have been relieved in 1999 to a larger extent for the grazed than for the ungrazed area, contributing to the difference in year-response between the areas. However, this effect was probably small compared to effects of the reed borer.

In this study, the effects of grazing by moulting Greylag geese in spring on biomass and nutrient dynamics of *P. australis* were quantified. Our data confirmed that grazing did not decrease NAPP. As expected, both annual N and P allocation to the shoots and annual above-ground N and P losses were higher in the grazed site. However, whereas we expected that these differences would be the consequence of increased regrowth after grazing, it seemed that one of the main mechanisms enhancing both NAPP as well as nutrient allocation and nutrient loss in grazed conditions occurred before the arrival of any goose in the area. The long-term effects of grazing on standing dead shoots probably relieved temperature-induced dormancy, increased incoming radiation and/or decreased insect damage early in the growing season, and this increased production between March and May with 50–100%. This result stresses the importance of long-term effects of grazing on (above-ground) biomass and nutrient dynamics in a field situation, even if no shifts in species composition or relative species abundance occur. Compensatory effects on the grazed reed were further enhanced by increased (re)allocation of resources above-ground, and this increased rhizome dynamics and turn over. Though resorption efficiency was increased for P and in 1997 also for N, overall nutrient losses were consistently much higher in the grazed than in the ungrazed reed vegetation. Despite increased relocation to above-ground plant parts and increased nutrient losses, rhizome nutrient storage over winter was not affected. Rhizome growth was enhanced during senescence from September to November, and this may explain some of the systematic discrepancy in grazing effects on below-ground storage between field observations and pot experiments, as the latter are usually harvested before onset of senescence.

It can be concluded that growth and nutrient dynamics of *P. australis* were enhanced rather than decreased by long-term effects of geese grazing in this eutrophic system. The impact of grazing was strongest on nutrient dynamics, and how this affects the nutrient cycling within the reed marsh should be the subject of further study.

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