

Rain limits food supply of temperate breeding Barnacle Geese *Branta leucopsis*

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The effect of rain on growth rates of individually marked shoots of a preferred food plant, Festuca rubra, was studied in a temperate Barnacle Goose brood rearing area during three consecutive years. We found that grass growth declined to zero well before fledging of the goslings during dry years, and that rain had an immediate short-term positive effect on grass growth, especially towards the end of the growing season. Experimentally we found some indication that water is limiting grass growth towards the end of the season. Besides that, there might have been an additional effect of adding droppings. Thus, rain is an important factor influencing grass growth rates, which in turn influence both quantity and quality of food plants. We propose such an effect as the mechanism explaining effects of rain on important life history parameters that have been documented earlier for this Barnacle Goose population, as well as in other herbivores.

Keywords: *Festuca rubra*, growth rate, temperate, rain, *Branta leucopsis*

Herbivores depend on the quantity and quality of their food plants. Biomass, growth rates, crude protein contents, and digestibility of grass species can be affected by many factors, such as genetic variation (Deinum & Struik 1989), temperature (Giroux & Bedard 1987), water supply (De Leeuw *et al.* 1990; Riley 1992), nitrogen mineralisation and fertiliser application (Bazely & Jefferies 1985; Hik *et al.* 1991; Manseau & Gauthier 1993), soil salinity (Zedler 1983; Srivastava & Jefferies 1995),

and herbivory itself (Ydenberg & Prins 1981; Cargill & Jefferies 1984b; Kotanen & Jefferies 1987; Bazely & Jefferies 1989a; Hik & Jefferies 1990; Bergeron & Jodoin 1993).

Geese (*Anser spec.*, *Branta spec.*) rely mainly on grasses, and the quality and quantity of preferred grass species can influence life-history traits such as fecundity and survival. For example, differences in food quality can affect body condition of adults (Coleman & Boag 1987; Larsson *et al.* 1998), which in turn

can affect breeding success (Ebbinge & Spaans 1995). Geese grow rapidly during the first weeks of their lives, and food quality and availability during this short period affect adult body size (Cooch *et al.* 1991; Larsson & Forslund 1991; Loonen *et al.* 1997b), as well as pre-breeding survival (van der Jeugd & Larsson 1998).

In many grass species a decline in growth rate occurs in the course of the season and this usually is accompanied by a decline in crude protein content and digestibility (Prop *et al.* 1980; Cargill & Jefferies 1984a; Prins & Ydenberg 1985). For herbivores, such as geese, this results in a peak in food abundance and quality early in the season. It has been suggested that the timing of nesting in geese has evolved to synchronise the hatching of goslings with peak food abundance and quality (Murton & Kear 1973).

A number of studies have shown that nitrogen may limit grass growth rates, and that geese might have a fertilising effect on the vegetation through their droppings (Bazely & Jefferies 1985; Madsen 1989; Hik & Jefferies 1990). Most of these studies relate to arctic areas, but in temperate areas other factors may limit grass growth, such as different components of the weather (Thorvaldsson 1987; De Leeuw *et al.* 1990). Geese breeding in temperate areas also face other constraints on growth and reproduction than geese breeding in the arctic. Previous studies on Barnacle Geese breeding on Gotland have shown that the nitrogen content in June of the main food plant, *Festuca rubra* L., was positively related to the amount of rain in May and June. Furthermore it could be shown that mean head length and tarsus length of cohorts of Barnacle Geese increased significantly with the amount of rain in May and June in the year of birth. Adult condition indices during moult were

positively related to the amount of rain in May and June in the year of capture (Larsson *et al.* 1998). In the present study, we propose a possible mechanism that can explain the patterns found by Larsson *et al.* (1998). Therefore we studied how rain influenced growth rates and the length of the growth period of the main food plant *F. rubra* on the major brood rearing area of Barnacle Geese on Gotland. We also performed an experiment, in which the effects of the addition of water and goose droppings on the growth rate of *Festuca rubra* were investigated.

Methods

Study area

We studied grass growth rate in three consecutive years, 1992, 1993 and 1994, on the peninsula Nārsholmen on the Swedish island of Gotland (57°17'N, 18°45'E) in the Baltic Sea. This peninsula is the main brood rearing area of the largest colony of the Baltic Barnacle Goose (*Branta leucopsis*, Bechstein) population. The Baltic Barnacle Goose population was naturally established in 1971 and has increased rapidly. In 1997 the population consisted of c. 17,000 individuals (Larsson *et al.* 1988; Larsson & Forslund 1994; Larsson & van der Jeugd 1998). During the period this study was undertaken, the colony increased from 1340 to 1730 breeding pairs (Larsson & van der Jeugd 1998). Barnacle Geese mainly feed on a narrow strip of saltmarsh at the edge of the peninsula. This is a *Festuca rubra* dominated saltmarsh, consisting mainly of the grass species *F. rubra* and *Agrostis stolonifera* (L.). The saltmarsh furthermore consists of *Poa trivialis* (L.), *Juncus gerardii*

(Loisel), *Potentilla anserina* (L.), and *Plantago maritima* (L.). *Puccinellia maritima* (Hudson) grows on a very narrow strip along the coastline. The vegetation of the peninsula has been grazed extensively by cows for many years.

In May the saltmarsh is used by arctic geese during their spring staging. During June and July the saltmarsh is heavily used by geese from the main colony. At the end of May the young hatch and are taken to the saltmarsh by their parents. They stay on the peninsula until the young fledge, around the 20 July. The main food plant during this period is *F. rubra*.

Grass growth rate measurements

We measured growth rate of *F. rubra* as total leaf elongation of individually marked shoots, and growth rates are expressed in millimetres per day. In all years and in all treatments, we measured 16 individually marked shoots in a small enclosure (0.5 by 0.5 m), at the same site on the peninsula every year.

We measured grass growth in 1992 between 3 June and 23 July, in 1993 between 28 April and 26 July, and in 1994 between 5 May and 22 July. We chose the position of the enclosures at a distance of about 10 meters from the shore line each year. Within the enclosure shoots were chosen that were approximately 10 cm apart. We marked shoots with small plastic rings around the stem. When a shoot lost its plastic ring and became unrecognisable we chose a new shoot.

We measured each leaf of a shoot from the point where it left the stem to the top of the leaf, in one millimetre intervals. Only the top leaf grows, and therefore individual leaves within a shoot can be followed

through the season. In 1992 we measured shoots twice a week, and in 1993 and 1994 about once a week.

Weather data were collected at the weather station in Herrvik, on the east coast of Gotland, 25 km north-east of N rsholmen. We calculated the amount of rain in an interval between two measurements as the cumulative rain from the day of the first measurement until the day before the second measurement of an interval.

Experimental design

In 1994 we carried out an experiment to assess the relative importance of water and droppings on the grass growth rate. At two different sites, ten and five meters from the shoreline, we put four enclosures (0.5 by 0.5 m) on the saltmarsh. At each site we used four different treatments. In all treatments growth rates were measured as described above. The control treatment did not receive any treatment. In the droppings treatment we added 10 fresh goose droppings at three-week intervals (5 May, 26 May, 16 June, and 7 July). In the water treatment we added 2 litres of water once a week, and the water and droppings treatment received both the water and the droppings treatment. The amount of droppings used in this experiment was about 2.5 times the average natural amount in this area, but was less than the maximum observed dropping density in this area (van der Veen unpubl.). The total amount of water added to the plots is approximately 3.6 times the average amount of rain in these three months. However, in the experiment this amount was added in pulses at weekly intervals, thus leading to considerable run-off. Therefore, the effectiveness of the water treatment is hard to interpret.

Table 1. Breeding phenology of Barnacle Geese, rain distribution over the season, and growth phenology of *Festuca rubra* on the brood rearing area of Barnacle Geese. End indicates when growth rates decreased to less than 0.2mm/day.

Year	Geese hatching	Monthly Rain (mm)				End of grass growth
		April	May	June	July	
1992	29 May	45	10	14	58	20 June
1993	28 May	19	12	39	51	26 June
1994	29 May	39	32	49	47	16 July

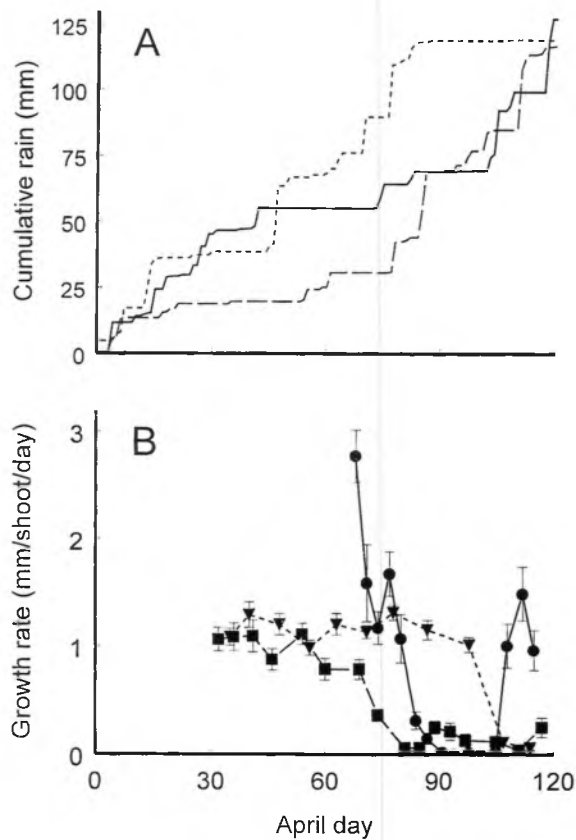


Figure 1. Cumulative rain from April to July (a), and growth rates of *F. rubra* (b) in 1992 (solid lines, circles), 1993 (striped lines, square), and 1994 (dotted lines, triangles), bars indicate standard errors.

Results

Direct effects of rain

The years 1992, 1993 and 1994 differed in the distribution of the number of days with rain over the months April, May, June, July (**Table 1**, ($\chi^2 = 17.77$, $df = 6$, $P < 0.01$), and often long periods of drought alternated with short periods with rain (**Figure 1a**).

The growth rate of *F. rubra* decreased during the brood rearing season to almost zero in all years (**Figure 1b**, **Table 1**, **Table 2**: season), but not at the same rate in all years (**Table 2**: season*year). The geese hatched their young around 29 May, and the young fledged about 20 July in all three years (**Table 1**). In 1992 and 1993 the grass stopped growing already early in the growth period of the goslings, while in 1994 grass growth did not decrease to zero until around the time of fledging (**Table 1**). Although only three data points were available for comparison, we correlated the amount of rain per month to the date at which grass growth had decreased to less than 0.2 mm per day. This correlation showed that the amount of rain in May might be a key factor for the length of the period of grass growth on N rsholmen ($R_s = 0.99$, $P = 0.09$), as opposed to the amount of rain in June ($R_s = 0.86$, $P = 0.35$) and April ($R_s = 0.08$, $P = 0.95$).

Besides the long-term effects of the amount of rain in May on the timing of the end of the growth period of the grass, we also investigated direct, short-term effects of rain on grass growth rates. Does rain result in rapid pulse of growth rate already within a measurement interval of a few days? Rain had a direct effect on grass growth rates over the whole season, but this effect differed between years (**Table 2**: rain, year*rain). In 1992 and 1994 there

was a positive direct effect of rain on leaf growth rate over the whole season, but in 1993 there was a negative direct effect of rain on growth rate over the whole season. This negative effect of rain on the growth rate might be explained by the different distribution patterns of rain over the seasons in the different years (see above) and the different effects of rain over the season on growth (**Table 2**: season*rain). We looked at this interaction by regressing growth rate on rain for each month separately. In both May and June the effect of rain on growth rate was not significant (May: $t = 0.67$, $df = 149$, $P = 0.50$; June: $t = -0.64$, $df = 253$, $P = 0.52$). However, in July there was a significant positive direct effect of rain on grass growth rate ($t = 2.13$, $df = 226$, $P < 0.05$). This suggests that in July grass growth is limited by water, and that even small amounts of rain can result in an increase in growth rate.

Experiment

An experiment was carried out in 1994 to examine the effect of water as well as the fertilising effect of goose droppings on growth rate of *F. rubra*. We used four treatments: control, droppings, water, and water and droppings at two different sites on the peninsula (5 and 10 meters from the shoreline). Since 1994 was a relative wet year and we only found profound effects of rain on growth rate in July, we only looked at how adding water and/or droppings affected the effect of rain on growth rate in July. There was a positive immediate effect of rain on growth rates (rain: $F_{1,371} = 229.91$, $P < 0.0001$). Growth rates were highest at the site closest to the shoreline (ANCOVA: $F_{1,371} = 4.01$, $P < 0.05$), but not significantly different between treatments (ANCOVA: $F_{3,371} = 1.97$, $P = 0.13$). However, the direct effect of

Table 2. Results of ANCOVA analyses of the effects of the covariate season (from May to July), the factor year (1992, 1993 and 1994) and the covariate rain (mm rain per measurement interval) on growth rates in each measurement interval of 16 *Festuca rubra* shoots. Non-significant interactions were removed from the ANCOVA model.

Factor	df	F	p
Season	1,630	205.56	<0.0001
Year	2,630	19.43	<0.0001
Rain	1,630	7.82	<0.01
Season*year	2,630	13.04	<0.0001
Season*rain	1,630	18.88	<0.0001
Year*rain	2,630	14.29	<0.0001

Table 3. Results of regression analysis of growth rate on rain for all four treatments in the experiment in July. Letters indicate significant differences between the slopes tested with a Tukey-Kramer a-posteriori test.

Treatment	Intercept	Slope	df	t	p
Control	0.007	1.572 (ab)	92	92.72	<0.0001
Droppings	-0.109	2.184 (a)	89	77.61	<0.0001
Droppings-and-water	0.127	1.821 (ab)	93	41.12	<0.0001
Water	0.142	1.151 (b)	90	44.86	<0.0001

rain on growth rates in July did differ between treatments (ANCOVA: rain x treatment $F_{3,371} = 3.80, P < 0.05$). In all four treatments the direct effect of rain was significant (**Table 3**), strongest in the droppings treatment, intermediate in the control and the droppings-and-water treatment, and weakest in the water treatment.

Discussion

This study shows that growth rates of *F. rubra* declined over the season. The date

at which the grass stopped growing appeared to be positively correlated with the amount of rain in May, although statistical power is weak due to only three data points. Apart from the long-term effect of rain on the end of the grass growth period, there was also an immediate effect of rain on growth rate of the grass, especially in July. Even within a few days following rainfall an increase in grass growth rate could be observed. The fact that the 16 shoots were chosen close to each other could potentially interfere with the assumption of statistical

independence of the 16 shoots within each enclosure. Dependence could arise because the shoots grew in the same microhabitat or because of high genetic similarity within the 16 shoots due to asexual reproduction. However, it is hard to imagine that the positive effects of rainfall on the growth rates of these 16 shoots, over a period of three months during three different years, would be an artefact. Therefore, in spite of the problem with independence, we think that our results are valuable in showing the mechanism behind the patterns found in Larsson *et al.* (1998).

A seasonal decline in growth rate of grass is a commonly observed pattern for forage plants grazed by geese (Prop *et al.* 1980; Cargill & Jefferies 1984a). However, in the Arctic, grass can continue to grow until well after fledging of the goslings (Gauthier *et al.* 1995). In our study, in two out of three years, grass growth rates decreased to almost zero already halfway during the period between hatching and fledging of goslings. This implies that, in dry years, Barnacle Geese breeding on Gotland experience low food quantity during the second half of the growth period of goslings.

Although rain in July did cause regrowth of the grass, growth rates were not as high as earlier in the season, before the drought. It has been shown in an experimental study that regrowth after autumn rain was dependent on the latitude of origin of different genetic strains of *Dactylis glomerata* (Volaire 1995). Strains from the Mediterranean were adapted to drought and showed high regrowth after autumn showers, while strains from northern latitudes showed only weak regrowth after drought.

In a previous study on geese breeding on Gotland it was shown that the nitrogen

content of the grass in June was positively related to the amount of rain in May and June. There was also a positive relationship between the amount of rain in May and June and the mean head and tarsus length of birth cohorts, and with body condition of the adults during moult (Larsson *et al.* 1998). Lower gosling growth rates result in smaller fledging size which leads to lower post fledging survival (Cooke *et al.* 1995; van der Jeugd & Larsson 1998; Loonen *et al.* 1999), as well as smaller adult body size (Cooch *et al.* 1991; Larsson & Forslund 1991), which in turn can affect fecundity (Larsson *et al.* 1998).

Thus, while breeding success in Arctic geese is largely dependent on the timing of snow melt (Prop & de Vries 1993), the amount of rain early in the breeding season seems to be an important factor influencing breeding success on Gotland. However, the extent to which drought is a limiting factor for reproductive success in arctic breeding geese is not clear, although Handa (1998) reports major growth responses of *Puccinellia phryganodes* after the addition of water in a study in the Hudson Bay. Most other studies on growth of food plants of Arctic breeding geese have not studied the effect of rain. In temperate regions drought is a well known factor affecting the growth rates of grasses (for example: Thorvaldsson 1987; De Leeuw *et al.* 1990; Riley 1992). It has been shown earlier that Barnacle Geese breeding on Gotland grow significantly slower than Barnacle Geese breeding on the arctic island of Spitsbergen (Loonen *et al.* 1997a). Several possible explanations have been put forward for these differences, like, lower nitrogen content of food plants on Gotland, higher competition for food due to higher population densities on Gotland, shorter daylight period on Gotland, and relaxed

selection for fast growth on Gotland. The early end of the grass growth period might be an additional possible explanation for the slower gosling growth on Gotland.

In July the plots in which water was added showed the smallest effect of rain, while the plots in which droppings were added showed the strongest effect of rain. The effect of rain in the other two plots was intermediate. Thus, at the end of the season, water seems to be limiting grass growth. Besides that, there might be an additional effect of adding droppings. However, problems of independence within the plots, as outlined above, are not as easy to dismiss as in the comparison between years. The fact that the 16 shoots within each plot were not independent might have exaggerated random differences among the plots.

The two sites differed in growth rate of the grass, with the site closest to the shoreline having the highest growth rate. The site closest to the sea probably had more access to water, due to its slightly lower elevation, and thus shorter distance to groundwater.

In our experiment fertilisation was done by using natural amounts of droppings. These amounts of droppings were high compared to studies in other goose-grazed areas, but the amount of nitrogen added was low compared to amounts used in agriculture. Nitrogen was shown to be limiting in the Arctic, and the addition of low quantities of nitrogen through faeces, still resulted in an increase in primary production (Cargill & Jefferies 1984a; Fletcher & Shaver 1983; Bazely & Jefferies 1985; Hik & Jefferies 1990; Hik *et al.* 1991; Manseau & Gauthier 1993). In other temperate areas results of experiments with natural amounts of dropping are

ambiguous. Some studies found no effect (Marriott 1973; Balkenhol 1984), while Madsen (1989) found a strong effect. Whether or not a response to the addition of goose droppings is evident depends upon the soil-nutrient status and the growth habit and phenology of the forage plants.

In summary, we found that grass growth declined to zero well before fledging in dry years, which might have repercussions on growth, body size, survival and even future fecundity of goslings. We also found that rain had an immediate short-term effect on grass growth, especially towards the end of the growing season. Finally, we found some experimental evidence that grass growth is indeed limited by rain towards the end of the growing season. We propose that rain can have profound effects on fitness of Barnacle Geese, and that such effects are mediated via effects on grass growth rates, which influences both quantity and quality of food plants. The importance of weather factors, such as rain, in explaining differences in reproductive success and population changes between years has been described in a number of herbivore studies (Albon, Guinness & Clutton-Brock 1983; Clutton-Brock *et al.* 1987; Owen-Smith 1990; Larsson *et al.* 1998), and perhaps requires more general consideration in interpreting of forage availability on reproductive success of herbivores.

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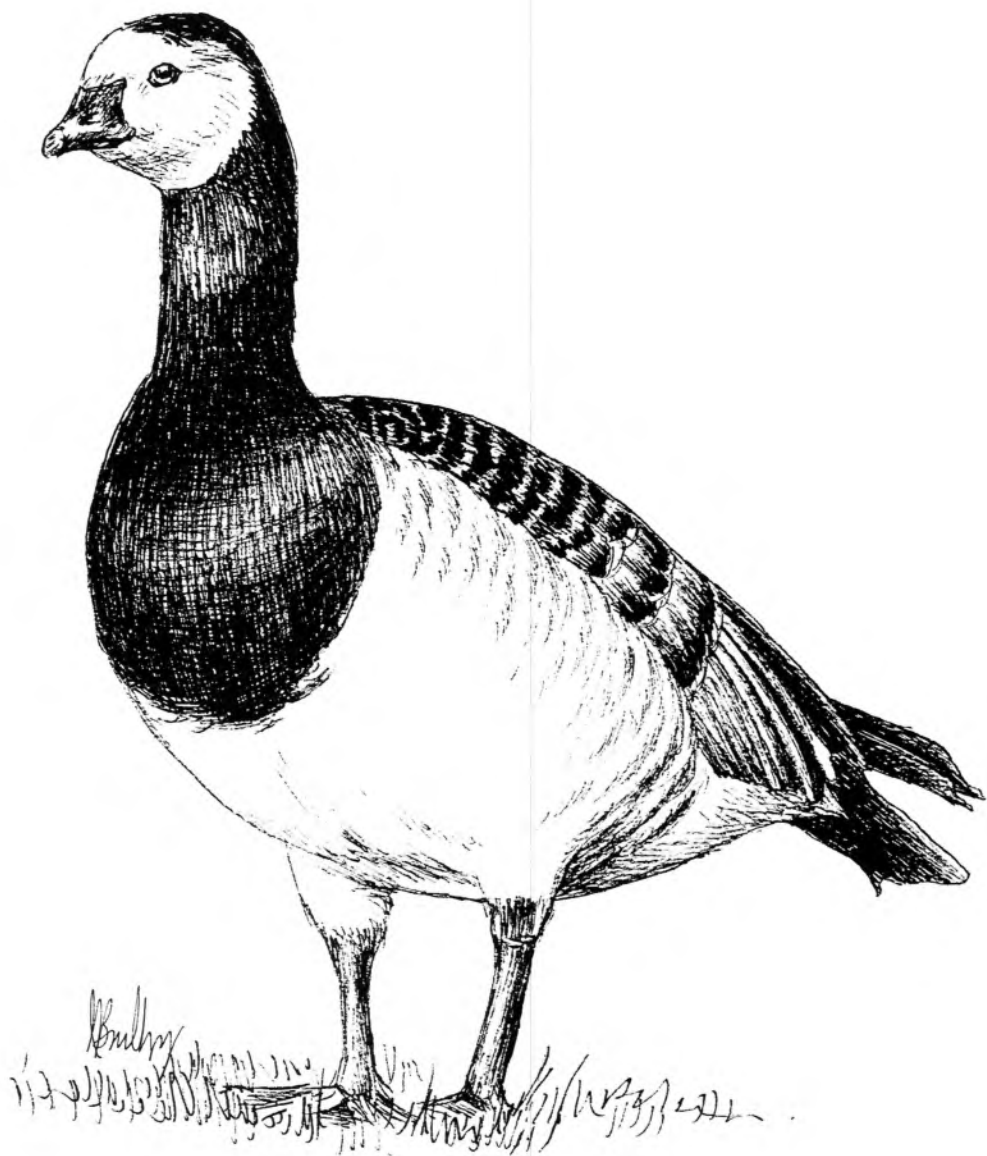
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Barnacle Goose *Branta leucopsis*
drawn by Amanda Bradbury, WWT