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THE INTERACTION OF BRENT GEESE BRANTA BERNICLA AND SEA PLANTAIN PLANTAGO MARITIMA DURING SPRING STAGING: FIELD OBSERVATIONS AND EXPERIMENTS

H. H. Th. PRINS, R. C. YDENBERG* and R. H. DRENT

Zoölogisch Laboratorium, Biologisch Centrum, Rijksuniversiteit Groningen, P.O. Box 14, 9750 AA Haren (Gr.).

SUMMARY

In spring, migrating Brent Geese (*Branta bernicla*) stage on the salt-marsh of Schiermonnikoog, a Dutch island in the Wadden Sea. During May, their principal food plants on the marsh are *Puccinellia maritima* and *Plantago maritima*. The Brent graze in large groups, and regraze the same places every four days. This interval seems to be related to the rate of regrowth of their food plants.

A close study of the grazing of *Plantago* by the Brent revealed that the bite size is about 14 mm and is almost exclusively confined to the youngest leaves. Each time the geese harvest about 30% of the rosette's leaf material.

A clipping experiment on the salt-marsh with *Plantago*, showed that a regime of harvesting about 30% of the rosette once every four days, like the geese do, gave the highest regrowth of new plant tissue, compared with no clipping, or with other clipping treatments.

The selective advantage to the individual in taking part in flock grazing movements is discussed in relation to the effects of Brent grazing on the vegetation.

1. INTRODUCTION

When one animal feeds on another the prey usually is killed. Herbivores, however, ordinarily forage in a highly selective manner, and consume only portions of their food (PRATT & GWYNNE 1977): the rest is not eaten and remains capable of regeneration. Predator-prey systems exist in which regeneration may be important (such as a bird exploiting earthworms, leaving a portion of each capture unconsumed, to regenerate a meal for another day (HARPER 1977) or reef fish "grazing" on corals and colonial hydroids). Regeneration with successive exploitation is, however, characteristic of many herbivore-plant systems, as has recently been underlined by MCNAUGHTON (1979).

A second salient feature of the herbivore-plant link concerns food quality. Vegetable material varies greatly in nutrient composition depending on the species, the part of the plant, and age, and is generally far less digestible than animal food. Carnivores conceivably select a diet on the basis of energy requirements and still end up with a diet balanced with respect to nutrients, because animal foods are of high quality (contain a high diversity of nutrients in readily digestible form). For herbivores, the relative importance of the two criteria may

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*Current address: Edward Grey Institute, Department of Zoology, South Parks Road, Oxford, Great Britain.

often be reversed and nutrient selection will dominate in determining the diet (White 1978).

Geese are true herbivores, but since they are incapable of digesting cellulose (Mattocks 1971) they follow the strategy of harvesting large quantities of relatively high quality forage each day to meet their requirements. Ebbinge et al. (1975) give a detailed description of the winter foraging routines of Barnacle Geese, *Branta leucopsis* (Bechstein 1803), and show that these birds consume more than 25 % of their body weight in fresh grass each day. Only one third of the caloric content is extracted and the bulk of the food passes through the intestinal tract in approximately 1.5 hours. These limitations underline the importance of food quality for the grazing tactics of geese. Particularly in spring, when high-arctic breeding geese lay down impressive reserves of fat and protein to allow reproduction in an environment still inhospitable at the time of arrival, the problem of nutrient selection may well be critical. Wypkema & Ankney (1979) have quantified the importance of protein uptake during spring migration for Snow Geese, *Anser caerulescens* (Linné 1758), by comparisons of carcass analyses of sample birds collected on different dates. We here present results from a complementary approach on another arctic-breeding goose species in the spring period, and examine the relations between the geese and their food stocks with two questions in mind. First, does selection of the diet maximise the protein intake? Second, does the grazing regime followed by the geese enhance the quality and/or quantity of the food resources? Results obtained with Brent observed in the northern Netherlands in May of 1978 will be presented here.

The dark bellied race of the Brent Goose, *Branta b. bernicla* (Linné 1758), winters mainly along coastlines of north-western Europe. Large numbers of these birds, whose total population has been increasing in recent decades, also winter in The Netherlands. Here they arrive chiefly in November, and depart again in the last days of May. Approximately seven hundred Brent spend each winter on the West Frisian Island of Schiermonnikoog. Based on ringsightings, it seems that the same birds return to Schiermonnikoog each winter.

From November until April, the geese forage in the island's polder, a large tract of dairy pasture. The polder contains a high density of food, and the birds mainly consume the grasses *Poa pratensis* L. and *Lolium perenne* L. Towards May there is a huge increase in the number of Brent; on some days in May about 10,000 geese can be observed. During this month, foraging activities are concentrated on the island's large (ca. 700 ha) salt-marsh. Here the principal food-plants are *Puccinellia maritima* (Huds.) Parl. and *Plantago maritima* L. Dijkstra & Dijkstra-De Vlieger 1980) and in some areas *Festuca rubra* L.

2. METHODS

Research was carried out in the spring of 1978 on the salt-marsh of Schiermonnikoog. During spring Brent mainly graze on the lower parts of the salt-marsh. To observe the pattern of goose visitation at one site, an area of about forty ha was selected (*fig. 1*). On the west and east this sample-area was bounded by

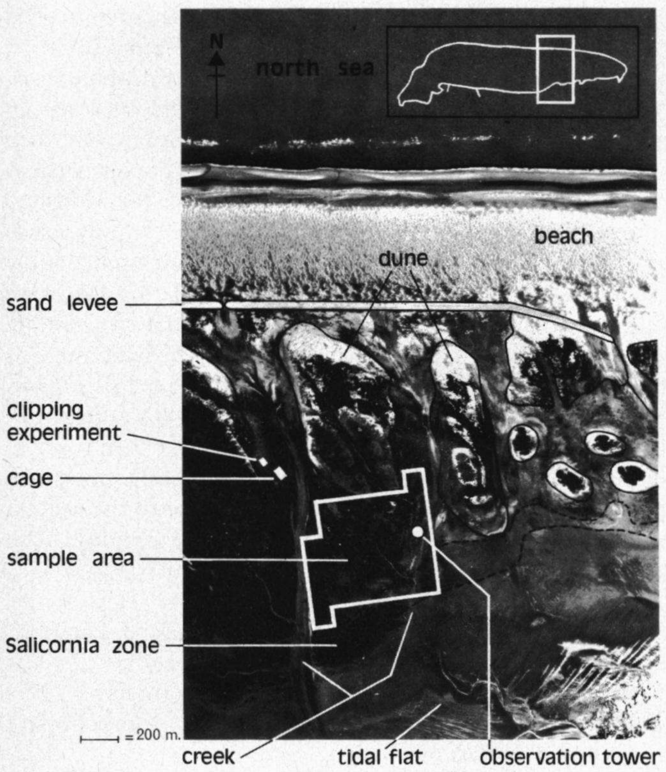

Fig. 1. Aerial photograph of the research area and its location on the island of Schiermonnikoog (insert).

creeks; in the south by a *Salicornia europaea* L. zone bordering the Wadden Sea and its tidal mud-flats, and in the north by some low dunes covered with *Ammophila arenaria* (L.) Link. The vegetation of the sample-area itself consisted of typical salt-marsh plants: *Plantago maritima, Puccinellia maritima* (which are food-plants of the Brent), *Spergularia media* (L.) C. Prest, *S. marina* (L.) Griseb. and *Artemisia maritima* L.

The sample-area was divided into square blocs of one ha each, the corners of which were marked with colour coded poles one metre in height, so each bloc could be recognized from a distance.

On the east side of the sample-area a four metre high observation tower was constructed. From this tower the sample-area was observed continuously from dusk to dawn in the period of 6–30 May 1978 with the aid of field-glasses (8–10 x) and telescopes (40–80 x).

During these observations all geese were counted and assigned to blocs every twenty minutes. These data made it possible to calculate the intensity of visitation in goose-minutes (EBBINGE et al. 1975) both for the different blocs and for the total sample-area.

To obtain an estimate of the amount the geese removed from their main food plant, *Plantago maritima*, we observed the grazing of three half-tame Brent on the salt-marsh, some 200 metres west of the sample-area (*fig. 1*). For this experiment, an area with an almost pure stand of *P. maritima* (about 1800 rosettes per m^2) was selected. In previous years and in the year of study Brent were seen foraging here quite regularly. A removable cage of netting was constructed, enclosing some 300 m^2, and the geese were allowed to graze here for 24 hours. Immediately before the start of the grazing period, a sample of 50 (ungrazed) rosettes was collected, while 50 (grazed) rosettes were sampled immediately afterwards. This experiment was repeated four days later. All rosettes were divided into subsamples consisting of the two upper leaves, the two middle leaves, and the bottom leaves. All leaves were measured to the nearest mm.

To get an idea of the effect of grazing on *Plantago*, a clipping experiment was designed. In an exclosure (to prevent grazing) on the salt-marsh, 40 rosettes of *P. maritima* were selected at random and divided into four groups of ten rosettes each. Each rosette was marked individually by a small numbered stick thrust into the ground. The length of every leaf of each rosette was measured to the nearest mm. This was repeated every fourth day during the following sixteen days. The treatments were as follows:

(c) no clipping (control group).
(i) all leaves longer than 10 mm had 10 mm removed; clipping on 9, 13, 17 and 23 May (light clipping, short interval).
(ii) treated as (i), but only on 9 and 17 May (light clipping, long interval).
(iii) all leaves longer than 5 mm were clipped back to a length of 5 mm; clipping dates as in (i) (heavy clipping, short interval).

In addition, a number of leaves were marked at 10 mm intervals with white Errorex marker. Distances between the marks were measured every fourth day in order to determine the distribution of growth over the leaf.

Plantago maritima had a constant dry weight per unit leaf length at this time of the year (0.137 mg/mm, $r = 0.731$, $n = 266$, $P < 0.001$) and so the above ground standing crop, harvest, and herbage accumulation (sensu Hodgson 1979) could be measured in mm and converted to dry weight. Since the density of *P. maritima* rosettes is known (18.1 rosettes/dm^2, S.D. = 2.25, $n = 10$) these parameters can be expressed as weight of dry matter per square metre (g d.m./m^2).

3. RESULTS

3.1. Goose visitation

Brent visitation at a single locality occurs as a series of discrete grazing peaks (*fig. 2*). The interval between peak days is rather constant in these data, *i.e.* each hectare-bloc was visited every 3.3 days, for a mean of 4.1 visits per hectare bloc for the 24 days covered by the observations.

Although obscured by the extreme degree of heterogeneity in the composition of the vegetation of the blocs, a relation between the duration of a single visit (in goose-minutes) and the length of the preceding interval can be established.

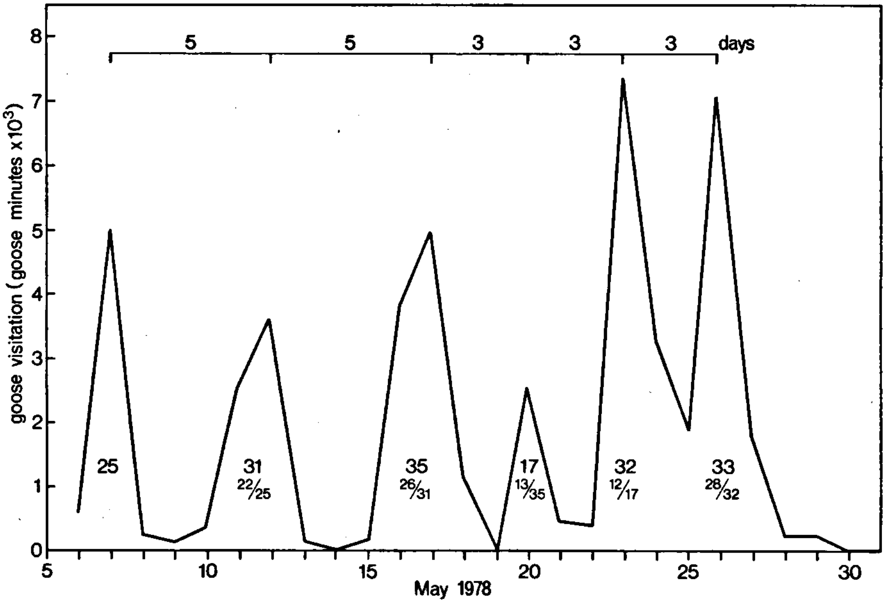

Fig. 2. The distribution of Brent Geese visitation time on the sample area each day during May 1978. Indicated along the top the interval in days between the "peak" days; numbers in each peak indicate the number of different hectare blocks visited, while the fractional number shows the rate of revisitation of hectare blocks grazed during the preceding peak.

Longer visits tend to follow longer intervals (*fig. 3*), suggesting that revisitation is markedly influenced by regrowth of food plants. Data on food intake in relation to the standing crop lead to the interpretation that the local food supply is

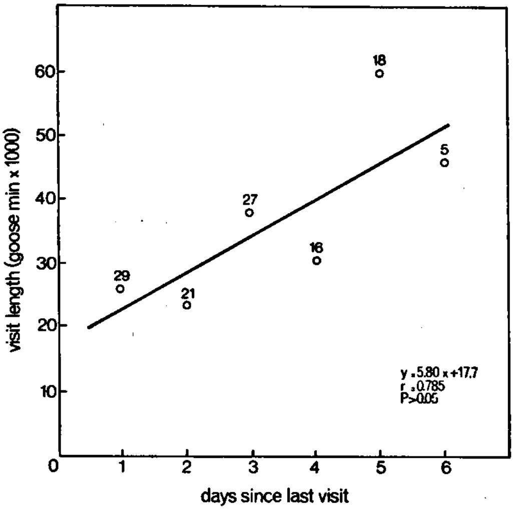

Fig. 3. The length of a single visit in individual hectare blocks as a function of the duration since the last visit. Numbers in the figure represent the number of hectare observations in May. Longer visits tend to follow longer intervals, suggesting that revisitation is controlled by regrowth.

depleted during each grazing peak, and that the interval between peaks corresponds exactly to the regrowth needed to allow the sward to be exploited again (DRENT & VAN EERDEN 1979). To test this hypothesis a fertilizer experiment was carried out in the same test area in 1979, and indeed the hectare blocs treated with inorganic nutrients showed an accelerated rate of growth (as measured by reflectance readings in exclosures). Observation showed that the interval between successive grazing peaks was greatly shortened on these treated blocs as compared to the surrounding controls, verifying that the pattern of visitation is dictated by the rate of regrowth (VAN EERDEN, in prep.). Implications of this cyclic pattern of grazing for the individual *P. maritima* rosette will be considered next.

3.2. Plant material removed per visit

Measurements on individual rosettes of *P. maritima* (*table 1*) before and after grazing by Brent show that material removed from the top four leaves accounted for upwards of 90% of the total leaf material taken per rosette. These top leaves lost about 13 mm each if grazed, while the amount of leaf material removed from the bottom leaves was only 1.5 mm (*table 2*, computed with the aid of data on incidence of grazing included in *table 1*).

Comparison of this estimate of the amount removed per blade with results from an indirect computation suggests that each peck or bite of grazing Brent constitutes one such leaf fragment when feeding on *P. maritima*. Bite size has

Table 1. Grazing by three half-tame Brent Geese of *Plantago maritima* on the salt-marsh of Schiermonnikoog. Experiment I on 24 May 1978; experiment II with the same geese on 28 May 1978.

	Experiment I			Experiment II		
	Leaf length of control	Leaf length of grazed rosettes	Removed	Leaf length of control	Leaf length of grazed rosettes	Removed
Youngest two leaves	13.7 mm (n = 94)	8.1 mm (n = 97)	40.8%	15.2 mm (n = 94)	9.1 mm (n = 99)	39.9%
Middle two leaves	20.7 mm (n = 94)	10.9 mm (n = 98)	47.5%	22.2 mm (n = 94)	8.9 mm (n = 98)	60.1%
Bottom	14.6 mm	14.1 mm	3.5%	16.1 mm	14.9 mm	5.6%

Table 2. Bite-size (mm/bite) of three half-tame Brent Geese foraging on *Plantago maritima* on the salt-marsh of Schiermonnikoog. Experiment I on 24 May 1978; experiment II with the same geese on 28 May 1978.

	Experiment I	Experiment II	Mean
Youngest two leaves	13.9 mm	14.1 mm	14.0 mm
Middle leaves	11.9 mm	12.1 mm	12.0 mm
Bottom leaves	0.9 mm	2.1 mm	1.5

been arrived at as follows. The captive Brent in the enclosure produced a dropping weighing 0.5 g (dry) on average every 390 seconds. When actively foraging the bite frequency was 2.63 bites/second, and the geese devoted 40 % of total time to foraging. The 390 seconds taken to form one dropping thus represents 390 × 0.4 × 2.63 = 410 bites. Since the digestibility of *P. maritima* on a weight basis was found to approximate 30% (based on digestibility trials utilizing natural markers in the diet undertaken by T. Boudewijn with the same individual geese on the same vegetation just prior to the grazing trials treated here) the average dropping corresponds to 14 mg dry weight intake of *P. maritima* (because each dropping represents the 70 % by weight nondigested residue). Since we know that the mean dry weight of *P. maritima* leaves was 0.137 mg/mm, we can now calculate bite size to be 12.7 mm (714 mg × 1/410 × 1/0.137 mg per bite).

Summing up, captive Brent in an enclosure of *P. maritima* utilized almost exclusively the upper, younger leaves, and removed approximately 14 mm of leaf length at each bite. These data will now be put into perspective in relation to clipping experiments on individual *P. maritima* rosettes.

3.3. Influence of clipping and grazing on the growth of P. maritima

By marking the individual leaves of rosettes of *P. maritima*, and then measuring the distance between the marks on different dates, it became clear that the growth zone of the leaf is mainly at its base (*table 3*). The growth in length diminishes both in the direction of the leaf tip and with time. When the leaves are clipped, the overall growth rate decreases, and the portion of tip growth decreases as well (*table 4*).

Clipping had no effect on the number of leaves per rosette (F-test; $P > 0.10$). On the average one rosette consisted of 5.8 leaves (S.D. = 1.0; n = 140).

Most forms of clipping gave an increase of total herbage accumulation (light clipping, with a long interval, i.e. ii) as compared with no clipping at all (control), or with another clipping treatment (heavy clipping, with a short interval, i.e. iii) (*table 4*). Total herbage accumulation is defined (HODGSON 1979) as the difference between the standing crops at the end and at the beginning of an experiment (no clipping), or as the sum of the herbage accumulations in the different intervals between clipping, measured by subtracting the standing crop at the end of the interval (immediately before clipping again) and the standing crop after the previous clipping. So these herbage accumulation figures are the net result of production of new material (growth) and losses.

The total harvest, defined as the total amount of material removed by clipping, did not differ significantly for the various clipping treatments (F-test; $P > 0.10$), but in course of time light clipping gave a more evenly distributed harvest than heavy clipping (*table 4*).

Clipping had a very pronounced overall effect on the production of new leaf tissue, as well as on the distribution of production within the rosette. In unclipped rosettes the production of new leaf tissue was rather evenly distributed over the different leaves, but an increased degree of clipping gave a shift of

Table 3. The growth of clipped and unclipped *leaves* of *Plantago maritima* (mm/day) in the period 9–20 May. The distance between the base and the first mark, and between the marks was 10 mm on 9 May; the distance between the second mark and the top was more or less 10 mm.

	unclipped		clipped	
Base-first mark	0.53 mm/day	79.5%	0.32 mm/day	93.1%
	(n = 26)		(n = 30)	
First-second mark	0.09	13.6%	0.02	6.9%
	(n = 23)		(n = 9)	
Second mark-top	0.05	6.9%	0.00	0.0%
	(n = 26)		(n = 20)	
Total	0.67	100.0%	0.34	100.0%

Clipped leaves were of rosettes of clipping treatment i.

Table 4. The harvest (mg d.w. per rosette) and total herbage accumulation (mg d.w. per rosette) of unclipped (c) and clipped rosettes of *Plantago maritima* (i, ii, iii) (see under Methods). The standard deviation is given in brackets.

	c	i	ii	iii
9 May	–	4.97 (1.93)	6.26 (1.08)	10.06 (2.59)
13 May	–	4.97 (2.53)	–	1.93 (0.54)
17 May	–	2.23 (1.63)	5.48 (1.58)	1.22 (0.19)
23 May	–	3.77 (1.90)	–	2.32 (0.73)
Total harvest	–	15.92 (5.94)	11.74 (2.03)	15.55 (3.27)
Total herbage accumulation in the period of 9–23 May	4.66 (2.77)	7.02 (2.65)	8.55 (3.24)	5.75 (1.37)

(The differences of total harvest between the treatments are not significant; t-test, $P > 0.10$. The differences in total herbage accumulation are significant for ii and c, and for ii and iii; t-test, $0.01 < P < 0.05$.)

production of new material from the bottom leaves towards the top leaves (*table 5*). Light clipping caused an increase in the production of new tissue (growth), but heavy clipping caused a decrease of growth. Intensive clipping led to a rejuvenation of the standing crop of *Plantago maritima* leaves (*fig. 4*).

Table 5. The influence of clipping (i, iii) (see under Methods) on the distribution of growth within the rosettes of *P. maritima*, and on the total growth, as compared with unclipped rosettes (c).

	c	i	iii
Top pair of leaves	31.5%	35.7%	63.3%
Second pair of leaves	34.1%	41.4%	30.7%
Bottom pair of leaves	34.4%	22.9%	6.0%
total growth of new leaf material (mg/day)	0.80	0.92	0.60

4. DISCUSSION

In plants two zones of intense growth can be distinguished, the apical meristem, and the leaf meristem. In monocotyledons such as the grasses, the leaf meristem is situated at the base of the lamina, while the apical meristem is enwrapped by the leaves. This protection of both meristemic zones renders grass well adapted to grazing, because normal grazing hardly damages the plant (SILSBURRY 1970; LANGER 1972). However, in most dicots, the leaf meristem is rather diffusely scattered through the leaf, and the apical meristem is rather exposed (SALISBURY & ROSS 1969). Therefore, these plants would seem to be less adapted to grazing. Nevertheless, in the dicotyledoneous *Plantago maritima* about 80% of the growth takes place at the base of the leaf, and the apical meristem is enveloped by the old leaves. Also, grazed leaves are capable of regrowth. Consequently *P. maritima*, like grasses, seems to be rather well adapted to grazing.

Calculations regarding the bite size of Brent Geese foraging on Sea Plantain, indicate that only the top four leaves of the rosettes are actively grazed. We conclude that Brent actively select only the four top leaves, which are the youngest, and sometimes unintentionally take an older leaf. During foraging each of the top four leaves is grazed individually. The geese removed about 30% of the rosette in one visit. In the field the geese revisited the same area once every four days on average. Observations of VAN EERDEN (pers. comm.) showed that about 80% of the plants are grazed during one single visit by Brent, so regrazing of the same rosette after an interval of four days is very probable. Regrazing of the same spot has been reported for a number of herbivores; for example: Giant Tortoise (*Geochelone gigantea*) (MERTON et al. 1976; HNIATUK et al. 1976), Hyrax (*Procavia johnstoni* and *Heterohyrax brucei*) (HOECK 1975); Sheep (HAFEZ et al. 1975; HODGSON 1966). For some of these animals a more or less regular revisitation, in one study on sheep of the same tiller (HODGSON 1966) has been reported.

Clipping, and by analogy grazing, had a clear effect on the age structure of the *P. maritima* leaf population (*fig. 4*). It led to a concentration of young tissue in the top leaves. Young plant tissue has a high proportion of protein and a low concentration of structural components (WILLIAMS 1975). Clipping will cause an increase of the concentration of soluble carbohydrates, phosphorus, calcium, and total digestible nutrients (COOK et al. 1958). A lowering of the concentration of structural components in the food results in a rise of the digestibility of this food for geese (WEIJAND 1976), so revisiting the same plants at appropriate intervals, instead of visiting new ones, will improve the quality of the uptake. This improvement could be demonstrated in grazed *Festuca rubra*, the main food plant of Barnacle Geese (YDENBERG & PRINS, in prep.).

Light clipping, i.e. removing 32% of the leaf material (about the same as the Brent removed), resulted in an increase of productivity, if clipping was done with a four day interval. No increase was found with a longer interval, and a decrease of productivity occurred under a heavy clipping regime (i.e. when 45% of the leaf material was removed each time). These clipping experiments suggest that Brent

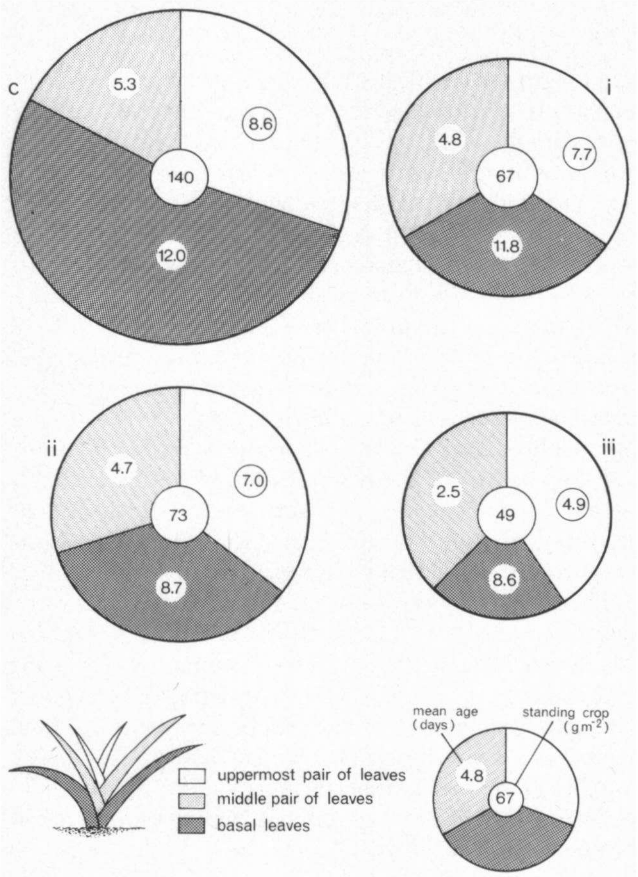

Fig. 4. The age structure of *Plantago maritima* leaf material in an unclipped situation (c), and under various clipping regimes (i = light clipping, four day interval; ii = light clipping, eight day interval; iii = heavy clipping, four day interval). Generally, increasing the intensity of clipping increases the proportion of young material, but reduces the standing crop. The standing crop at the end of the clipping intervals on 23 May is given (see key at bottom).

optimize growth, and return to harvest the protein-rich and readily digestible fresh leafy material at the appropriate interval. Although we have good field evidence for the effect geese have on enhancing the quality of their food supply by successive grazing (i.e. the geese manipulate the age distribution of the leaves and maintain the vegetation at a growth stage allowing maximal extraction of protein) so far direct proof that growth stimulation plays a role has not emerged from the field data (YDENBERG & PRINS, in prep.). The close correspondence of the grazing impact normally exerted by Brent with the maximal productivity of the clipping experiments can hardly be fortuitous, however, and we incline to the viewpoint that our field data have so far been too crude to reveal the growth stimulation that must be taking place. Further work is planned to determine how the grazing interval is determined (allowing regrowth to occur but harvesting before a marked decline in food quality has taken place, i.e. reaching a compromise between potential food intake and its quality).

The effects of Brent on *P. maritima* suggest why it is of selective advantage to the individual to take part in flock grazing movements so typical for geese. Group grazing, following a peaked pattern of visitation, will result in local areas in which all food plants are growing in phase. Because of this synchrony, the geese need not waste time locating plants in the right stage of growth during a repeat visit, as it will not be necessary for each individual to revisit the same individual plants to benefit from the enhanced quality of recent regrowth.

In effect, the goose flock functions as an integrated harvester, enabling a more consistent return of high quality herbage to the individual contrasted to solitary strategies of harvesting vegetation. The flock habit ensures a stepwise gradation of food patches differing in date of harvest and hence in potential yield to the geese. Selection of food patch on a day to day basis is thus vastly simplified as the relatively large differential between adjacent patches can quickly be ascertained by scouting goose groups early each morning. In this sense our view of how goose flocks function is an extension of the argument put forward by CODY (1971). Cody observed the depletion of seed stocks by wandering finch flocks, and pointed out that the flock habit would cause uniform depletion over large areas, making discovery of unexploited areas on following days more efficient. Interpretation of flock function in geese awaits observation on intake rate, selectivity, and search path of individually marked birds before further speculation can be profitable.

Recently MCNAUGHTON (1979) has presented preliminary data on stimulation of above-ground productivity in grassland plots in the Serengeti dominated by *Andropogon greenwayi*, when grazed by large migratory herbivores. As in our clipping experiments, an optimal grazing intensity can be determined, corresponding to a maximal production in biomass terms. McNaughton points out that his field estimate of grazing pressures actually exerted by wildebeest (*Connochaetes taurinus*) herds is far in excess of this biomass optimum, and he speculates that nutrient yield may be the quantity that is optimized. Apparent overcropping may in fact provide food of the highest quality (youngest growth stage) at the expense of total biomass increment. These observations on *Andropogon* call for extensive experimental manipulations by clipping before the functional significance of the food/herbivore link can be fully interpreted, and McNaughton has already embarked on such a programme. We hope to have shown that these same features are available for study in many other ecosystems on our very doorstep.

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