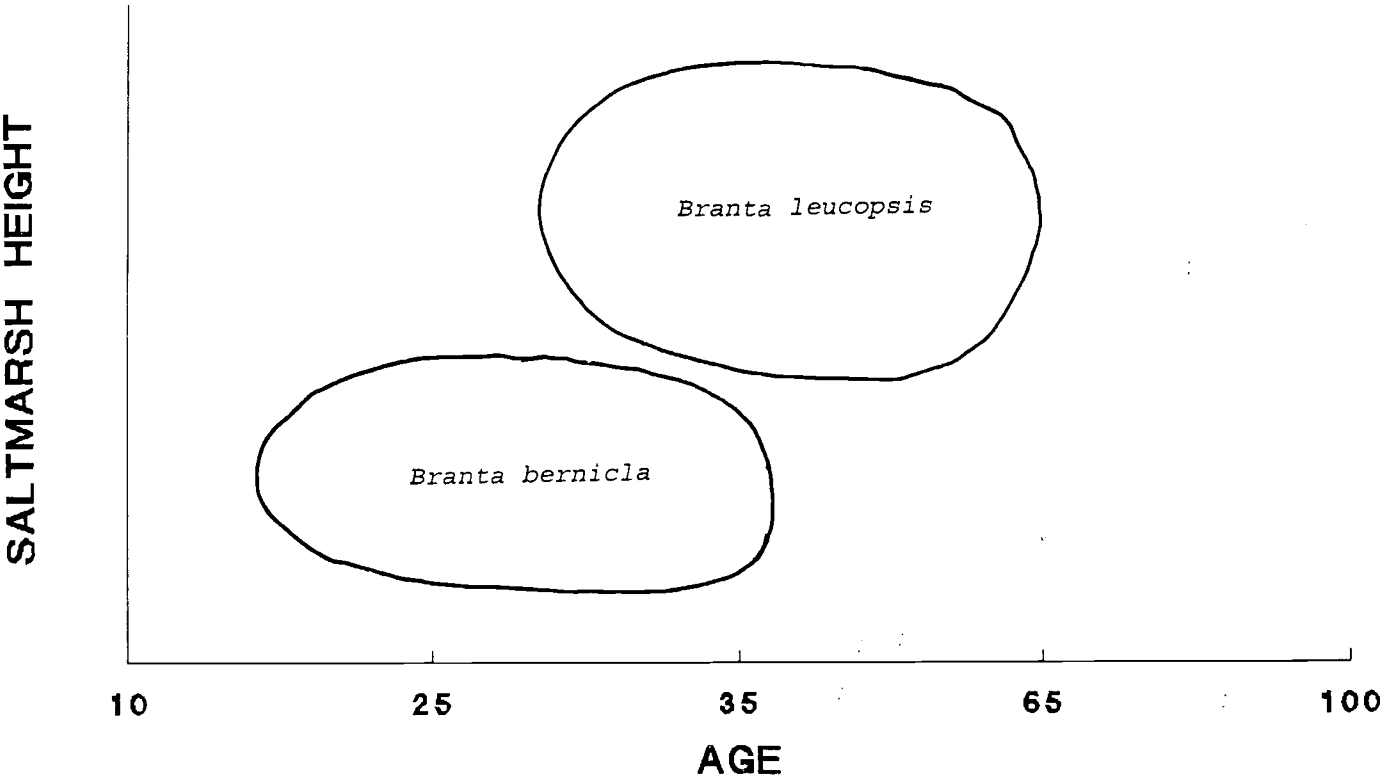
HERBIVORY AND VEGETATION SUCCESSION ON THE SCHIERMONNIKOOG SALTMARSH.



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CONTENT.

SUMMARY

Barnacle *Branta leucopsis* and Dark-bellied Brent Geese *Branta bernicla* forage during vegetation succession on the saltmarsh of Schiermonnikoog. The amount of dead material increases during vegetation succession. The productivity and peak standing crop are increasing until a maximum is reached after 65 years of vegetation succession. The Barnacle geese forage on the high and middle saltmarsh between 25 and 65 years of succession. The Brent geese forage on the middle and low saltmarsh between 10 and 35 years of succession.

TERMINOLOGY.

In the past, 'vegetation' and 'succession' have been used often in literature although the meaning of these terms is confusing. Van Andel *et al.* (1993) reviewed the concepts concerning vegetation and succession and created some order in the use of these terms as summarized here.

Vegetation is composed of *populations* of plant species and of plant *individuals*. Westhoff's (1979) definition of vegetation includes both aspects: 'A system of largely spontaneously growing plant populations (Van Andel *et al.* (1993) prefer plant individuals) growing in coherence with their sites and forming part of the ecosystem together with their site factors and all other forms of life occurring in these sites'.

Van Andel *et al.* (1993) start from Pickett *et al.*'s (1987) proposal to distinguish between pathways, causes, and mechanisms of vegetation change to describe, explain or predict aspects of succession: (a) *pathway* is the temporal pattern of vegetation change; (b) *cause* is an agent, circumstance or action responsible for successional patterns; (c) *mechanism* is an interaction that contributes to successional change. Consequently, a successional sere is a particular type of pathway, which might depend on particular sets of causes and/or mechanisms. Further, it is confusing to relate mechanisms of succession to kinds of succession (such as primary and secondary succession).

This leads to propose the following framework:

(1) Interactions between plants, i.e. autogenic processes, will be termed *vegetation mechanisms of succession* (for example seed banks, establishment, facilitation, competition).

(2) Effects of biota other than higher plants within a community will be treated under the heading 'biogenic *causes* of vegetation succession' (for example vertebrate and insect herbivores, parasitism, food webs).

(3) If autogenic mechanisms and allogenic causes are no longer distinguishable and it is particularly the interaction between these two that governs succession, '*ecosystem mechanisms of succession*' are discussed (for example dune valleys, moist grasslands, saltmarshes, mire systems).

INTRODUCTION.

Herbivory and (primary) vegetation succession on the saltmarsh has been studied recently by Olff (1992). The saltmarsh on the eastern part of Schiermonnikoog is a unique example of (primary) vegetation succession, because it is relatively unaffected by man. Geese forage on the saltmarsh during spring staging. The island is gradually moving eastwards, which resulted on the saltmarsh of Schiermonnikoog in a gradient of various stages of increasing development situated adjacent each other (i.e. chronosequences) from east to west.

It has been shown recently that spatial saltmarsh zonation (with the highest parts being the oldest (Chapman 1974, Bakker 1989)) does not reflect the succession (or chronosequence) on Schiermonnikoog (Roozen & Westhoff 1985, De Leeuw *et al.* 1993). The zonation is formed by a height gradient in base elevation (De Leeuw *et al.* 1993), which leads to differences in salt concentration and inundations. Zonations with the same inundation frequencies can be compared with each other. This implies that succession can be studied at the high, mid and lower saltmarsh.

Primary vegetation succession starts with bare mineral soil, which is initially devoid of organic humus and plant propagules (Tilman 1988), and during succession nutrients accumulate. The major soil factor limiting plant growth is nitrogen (Lawrence 1979, Tilman 1985, 1988). Saltmarshes are often regarded as environments in which nitrogen availability is a limiting factor to plant growth (Valiela & Teal 1974). Tidal inundations cause deposition of clay. In time and place, the clay deposition increases from the high to the low saltmarsh. Olff (1992) found a linear relationship between the claylayer thickness and the amount of nitrogen in the upper 50 cm (corrected by Van Wijnen 1993).

DeAngelis (1992) expected that the primary production in very early successional stages will be too low to sustain herbivory. The density of herbivores above a certain threshold is expected to be positively related to the level of primary production (Oksanen *et al.* 1981, McNaughton *et al.* 1989). At high levels of primary production, the herbivore density is expected to decrease, due to either predator control of herbivores (Hairston *et al.* 1960, Oksanen *et al.* 1981) or due to decreasing quality (N content, digestibility), which leads to replacement of small plants by taller plants (Tilman 1985). Studies in East- Africa (Vesey-Fitzgerald 1960, Bell 1970, McNaughton 1976) have demonstrated that the movements of large herbivores are dependent on seasonal concentrations of nutritious vegetation.

Spring staging Barnacle *Branta leucopsis* and Dark-bellied Brent Geese *Branta bernicla* forage on the saltmarshes. Prior to migration to the arctic breeding areas, geese have to deposit large amounts of body reserves, because the condition at the moment of departure to the breeding grounds is a factor, which correlates with reproductive success (Newton 1977, Ebbinge *et al*. 1982, Thomas 1983, De Boer & Drent 1989). Conditions for this are favourable in spring due to increasing day length and the onset of plant growth. Several studies showed the importance of high quality food during spring staging (Wypkema & Ankney 1979, McLandress & Raveling 1981, Ydenberg & Prins 1981, Thomas & Previtt 1982, Thomas 1983, Boudewijn 1984, Davies & Cooke 1983, Prop & Deerenberg 1991).

This leads to the following hypothesis. During vegetation succession, the availability of limiting nutrients in the soil increases. Therefore, the productivity will increase during vegetation succession. A low or a high productivity can exclude herbivory. The density of herbivores can also be restricted by other factors (quality and abundance of food plants, vegetation density).

There will be looked at some general features of the saltmarsh succession (bare soil, productivity, peak standing crop, nitrogen content) and the occurrence of the Barnacle and Brent Geese during spring staging.

SITE DESCRIPTION.

Study area.

Research was carried out from March to August 1993 on the eastern saltmarsh of Schiermonnikoog (Figure 1), one of the Dutch Frisian Islands (53°30'N, 6°10'E). One of the methods to describe vegetation succession is by using chronosequences (Crocker & Major 1955, Olff 1992). The chronosequence consists of five successional stages (i.e. 10, 25, 35, 65 and 100 years).

Figure 1. The Schiermonnikoog study area.

Saltmarsh morphogenesis (After Olff 1992).

The process of saltmarsh formation on Schiermonnikoog differs from mainland saltmarshes (De Leeuw *et al.* 1993). On coastal islands (Figure 2), most elevational variation is caused by primary dune formation on the beach. In the first stage, small dunes are formed on bare strand plates, mainly due to sand catching by *Elymus farctus*. During the next stage, mainly annual species establish which prevent the sand from blowing. Meanwhile, tidal inundations cause deposition of clay, where the rate of deposition is probably highest in the intermediate zone. The tidal flats are daily inundated, preventing plant growth, while the highest dune areas are almost never inundated. Different stages of saltmarsh development can be found next to each other on Schiermonnikoog, since currents cause the island to move eastwards. Therefore, the western part of the island is the oldest part. The young stages can be found in the eastern part. This process was quantified by mapping the vegetated areas from aerial photographs, which were taken in 1927, 1952, 1969 and 1980. Furthermore a topographical map (with a good indication of the vegetated areas) dating from 1854 was used.

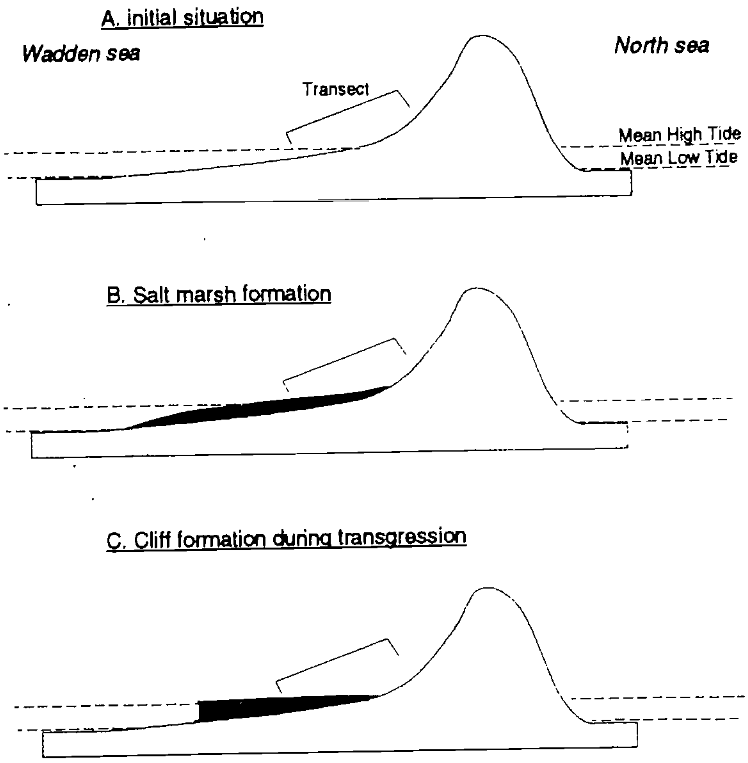

Figure 2. Schematic representation of saltmarsh formation on coastal bar islands. The black layer represents the organic matter containing sediment which is deposited on the sandy subsoil by tidal inundations (from Olff 1992).

Five transects are used for this research. The transects represent sites of different periods of saltmarsh development and the vegetation succession is estimated to have progressed for 10 years (transect 1), 25 years (transect 2), 35 years (transect 3), 65 years (transect 4) and 100 years (transect 5). The transects are located on the higher parts of the gradient. At each successional stage a transect (10x50m) was set out by Olff (1992) and co-workers. Two rows of sample points were placed at regular distances (5m). The elevation (according to the Dutch Ordnance Level (NAP)) and clay accretion was measured by Olff and co-workers.

Plant species distribution.

The saltmarsh vegetation of Schiermonnikoog has been described in several studies (Dijkema & Wolff 1983, Bakker 1989, Westhoff & Van Oosten 1991, Olff 1992).

The lower part of the gradient was initially dominated by *Puccinellia maritima*, *Suaeda maritima* and *Glaux maritima*. *Limonium vulgaris* quickly increased during succession on this lower part, while initial dominants disappeared. *Limonium* was followed up by *Artemisia maritima*, which species was finally replaced by *Atriplex portulacoides*, and *Elymus athericus*. *Plantago maritima* was characteristic for the early stages of succession on the middle part of the gradient, where it was followed up by *Festuca rubra*.

The highest parts of the gradient were dominated by *Armeria maritima* and *Festuca rubra*. *Armeria* gradually disappeared while *Festuca* remained dominant. *Elymus athericus* finally became dominant over large parts of saltmarsh, where it initially only was found on the highest parts. This was also observed for *Limonium vulgaris*, *Atriplex portulacoides* and *Festuca rubra*.

MATERIAL & METHODS.

Vegetation sampling.

In spring every three weeks and in the summer every six weeks (Table 1) vegetation samples were taken at the five successional stages at three different zonations (low, middle and high) to measure standing crop. The samples were taken next to the five transects to relate the vegetationsamples with the droppings in the transects. It was not possible to take samples inside the transects, because the transects are also used as permanent plots. It is assumed that the vegetation was homogenous at each of these 15 sites . This means that there are no differences between the vegetation inside and next to the transects. At all 15 sites five samples were collected in a three week exclosure using a 15 cm diameter (soil) corer. Exclosures were made of chicken wire (enclosed area = 1 m^2 and mesh width 3*3 cm) to exclude grazing by large herbivores and minimize wind and micro-climate effects. The samples were collected and sorted out within three days to minimize effects on biomass and nitrogen content. Each sample was sorted into dead plant material, *Festuca rubra*, *Puccinellia maritima* and the remaining fresh material. The samples were dried for 24 hours at 60°C and weighed to the nearest 0.01 gr. A regression was performed from week 17 until week 30 on the biomass-data to calculate the biomass increase per week. The collected samples of the 10, 25 and 100 years old saltmarshes of week 11 and 14 were left out, because there was no sampling at 35 and 65 year old saltmarshes.

week	date
11	19-21 March
14	9-12 April
17	30 April- 2 May
20	21-23 May
23	11-13 June
30	28-30 July

Table 1. Sampling dates in spring and summer 1993.

Species abundance.

Plantcoverage was estimated were recorded in the tempory exclosures according to the Point-Quadrat Method at every site before sampling. A sharp pointed metal pin was allowed to reach the vegetation. The first hit was recorded (plants species, soil or dead material). At all 15 sites, 100 points were sampled. Only the principle foodplants of the Barnacle and Brent geese will be discussed here (i.e. *Festuca rubra*, *Puccinellia maritima*, *Plantago maritima*, *Triglochin maritima* and *Elymus* spec.). Only the coverage of *Elymus* spec. in week 30 is shown, because than the coverage is maximal. The 'coverage' of the soil in week 14 is shown to illustrate the increasing vegetation coverage.

F. rubra, *Pu. maritima*, *Pl. maritima* and *T. maritima* were restricted to one or two zonations. *F. rubra* and *Pl. maritima* is restricted to the high and middle saltmarsh, *Pu. maritima* and *T. maritima* to the low saltmarsh.

Nitrogen analysis.

The five samples per site were pooled, grounded to pass a 1 mm sieve and analyzed for total nitrogen content by using the Kjelldahl-Deys technique. Material, not sufficient for nitrogen analysis, was left out. The nitrogen concentration of the four categories and the amount of nitrogen per squared meter is calculated. The nitrogen concentration of *F. rubra* and *Pu. maritima* will be divided into three periods: period 1 (week 9-14), period 2 (week 15-17) and period 3 (18-23).

Geese and dropping counts.

Goose flocks are counted during fieldwork. These counts do not reflect the real numbers of geese on the island, but can be used as an index to appoint the arrival and departure of Barnacle and Brent Geese.

Geese droppings are counted and collected weekly as a measure of grazing pressure at the five successional stages. At every plastic tube geese droppings are collected in circular plots of 4 m^2 using a 1.13 m long rope. The grazing-pressure of each site can be calculated as droppings per square meter per unit of time. The geese droppings are pooled per height. The occurrence of the geese on the saltmarsh will be divided into three periods: period 1 (week 9-14), period 2 (week 15-17) and period 3 (18-23).

RESULTS.

Plant Abundance (according to the Point Quadrat Method).

The coverage *Festuca rubra* on the high and middle saltmarsh during spring is shown in Figure 3. In spring, the highest coverage on the high saltmarsh is reached at the young (10 and 25 years) saltmarsh. On the 35 and 65 years high saltmarsh is hardly any coverage of *F. rubra* found. The peak coverage of *F. rubra* on the high 25, 65 and 100 years high saltmarsh (resp. 81%, 22% and 35%) is reached at week 20 and on the 10 (39%) years high at week 30. On the middle saltmarsh, the highest coverage of *F. rubra* is reached at the 25, 35 and 100 years middle saltmarsh. On the 10 and 65 years middle saltmarsh, the coverage of *F. rubra* is low. The highest coverage of *F. rubra* were reached on the 25 and 35 years middle saltmarsh (resp. 64% and 53%) and on the 100 (83%) years middle saltmarsh at the end of May.

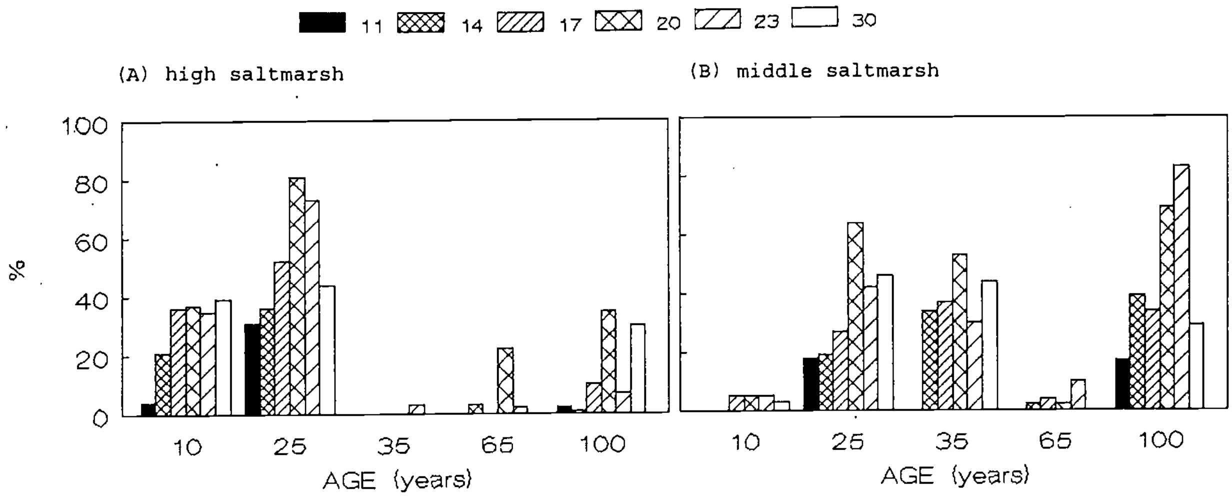

Figure 3. The coverage of *Festuca rubra* on the (A) high and (B) middle saltmarsh.

The coverage of *Puccinellia maritima* is maximal at the youngest stage (Figure 4). The highest coverage of *Pu. maritima* is found at the 10 years low saltmarsh and the peak coverage (56%) is reached at week 20. On the 10 years middle and high saltmarsh, the coverage of *Pu. maritima* reaches approximately 20-25 % during spring. At older stages, a far lower coverage of *Pu. maritima* is found.

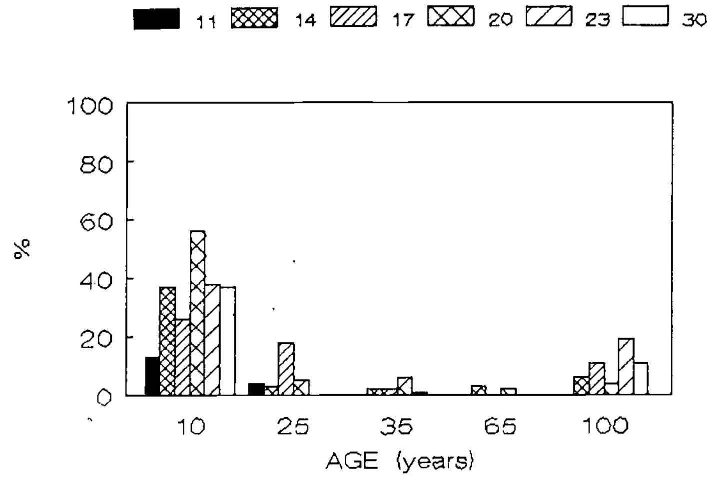

Figure 4. The coverage of *Puccinellia maritima* on the low saltmarsh.

Only on the 10 and 25 years high saltmarsh *Pl. maritima* is found (Figure 5). At both transects, the coverage of *Pl. maritima* increases during spring and the peak coverage of 10 and 25 years high saltmarsh (resp. 24 % and 14 %) is reached at respectively week 30 and week 20. *Pl. maritima* is only found on the 25 years middle saltmarsh, increases during spring and reaches peak coverage (42%) at week 30.

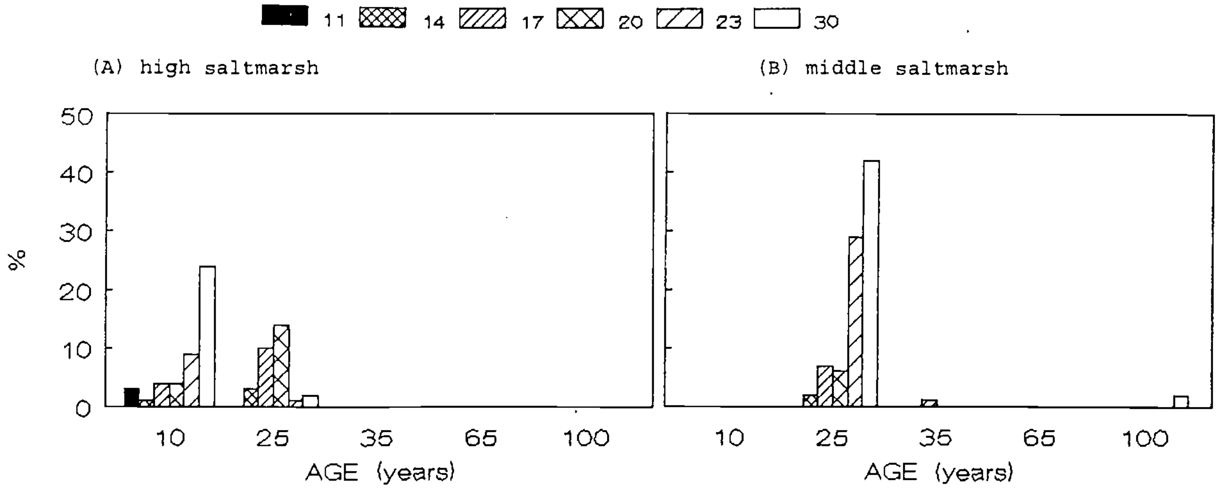

Figure 5. The coverage of *Plantago maritima* on the (A) high and (B) middle saltmarsh.

The coverage of *Triglochin maritima* (Figure 6) on the low saltmarsh is less than 6%. The coverage of *T. maritima* on the low saltmarsh varies between 2% (25 years) and 5% (100 years). *T. maritima* was hardly found on the high and middle saltmarsh and therefore not shown.

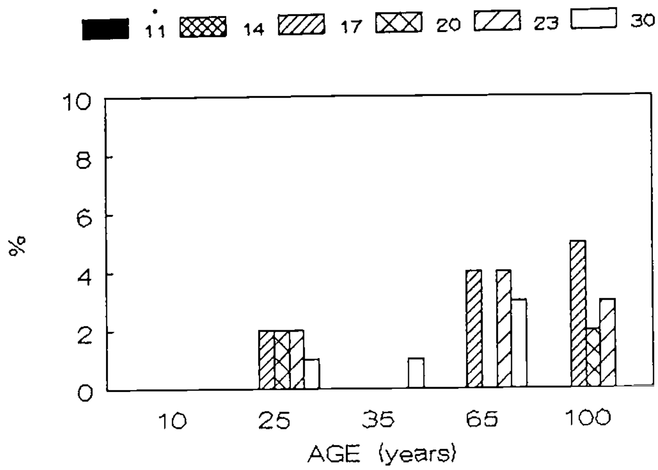

Figure 6. The coverage of *Triglochin maritima* on the low saltmarsh.

Elymus athericus is only found at the 35, 65 and 100 years old high saltmarshes (Figure 7). The coverage of *Elymus athericus* increases during the spring and reaches a peak coverage (resp. 91%, 87% and 62%) at week 30.

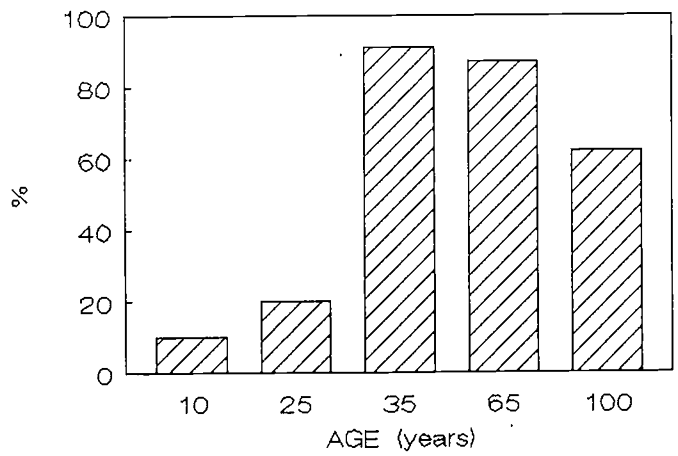

Figure 7. The peak coverage (week 30) of *Elymus athericus* on the high saltmarsh.

Primary succession starts with bare soil (Van Andel *et al.* 1993). Early in the season, the coverage of bare soil (Figure 8) shows a decreasing trend for the low, middle and high saltmarsh during succession with respectively $r_{low}=-0.77$ $p=0.063$ $n=5$, $r_{middle}=-0.65$ $p=0.12$ $n=5$ and $r_{high}=-0.80$ $p=0.053$ $n=5$.

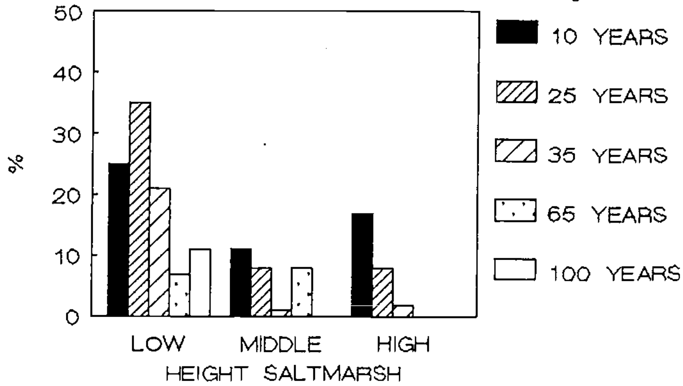

Figure 8. The coverage of bare soil (week 14) on the low, middle and high saltmarsh.

Biomass and productivity.

As an estimation of the productivity quantify, the peak standing crop was taken for each zonation in the succession during the season. The peak standing crop at all three zonations (Figure 9) increases during succession until 65 years of succession (resp. $y_{low}=323.1+2.2x$, $n=20$, $r=0.47$, $p<0.05$; $y_{middle}=82.7+6.9x$, $n=20$, $r=0.94$, $p<0.001$; and $y_{high}=97.7+3.4x$, $n=20$, $r=0.62$, $p<0.01$). The peak standing crop of the 65 years old low (465.5 $gr/m^2 \pm$ SE 60.5) and middle saltmarshes (531.5 $gr/m^2 \pm$ SE 30.4) are significantly higher than of 100 years low and middle saltmarshes (resp. 259.1 $gr/m^2 \pm$ SE 33.6 and 350.4 $gr/m^2 \pm$ SE 21.8) (ONEWAY SNK, $p<0.05$). The 100 years high saltmarsh (243.6 $gr/m^2 \pm$ SE 45.4) does not differ significantly from the 65 years high saltmarsh (312.1 $gr/m^2 \pm$ SE 76.7).

The percentage fresh material (Figure 10) during succession decreases on the lower and higher saltmarsh (resp. $y_{low}=0.80-0.05x$, $n=75$, $r=0.43$, $p<0.001$ and $y_{high}=0.83-0.13x$, $n=75$, $r=0.74$, $p<0.001$). The percentage fresh material on the middle saltmarsh tended to decreases, but not significantly ($p=0.1189$). The 10 year old low saltmarsh has a significant higher percentage fresh material than the older low saltmarshes (ONEWAY-SNK, $p<0.05$). The transects of respectively 10 (72.0 % $\pm$ SE 4.1) and 25 (61.1 % $\pm$ SE 5.3) year old high saltmarsh have significantly higher percentages than respectively the 35 (42.7 % ± SE 2.2), 65 (26.2 % ± SE 4.9) and 100 (26.6 % ± SE 3.5) years old. The 35 years old high saltmarsh have also a significantly higher percentage fresh material and 65 and 100 years old high saltmarsh.

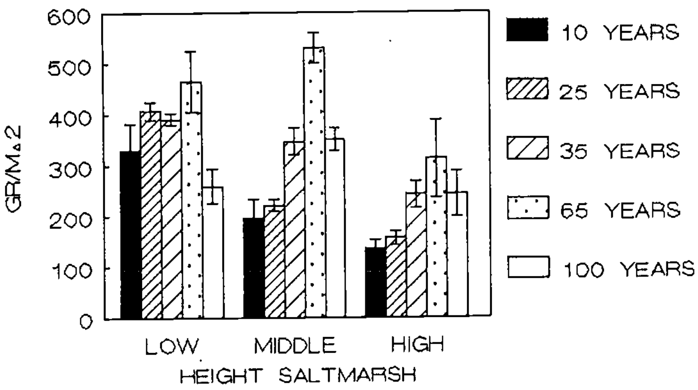

Figure 9. The peak standing crop (alive) on the low, middle and high saltmarsh.

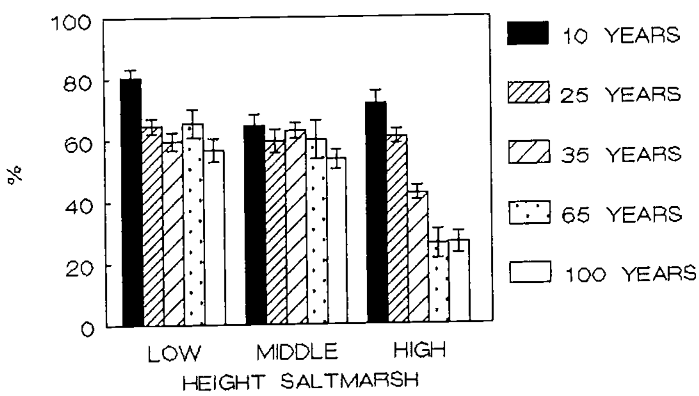

Figure 10. The percentage fresh material on the low, middle and high saltmarsh.

The biomass of *F. rubra* (Figure 11) increases in spring on the middle and high saltmarsh. The biomass on the 35 and 65 years high saltmarsh is small. The peak biomass of *F. rubra* on the 10 (45.57 gr/m² ± SE 5.42), 25 (113.58 gr/m² ± SE 15.03) and 100 (77.31 gr/m² ± SE 25.86) high saltmarsh is reached in respectively week 23, 23 and 20. The peak biomass of *F. rubra* on the 10 (24.53 gr/m² ± SE 9.05), 25 (97.07 gr/m² ± SE

16.60), 35 (134.04 gr/m² ± SE 35.29) and 100 (153.57 gr/m² ± SE 26.32) years middle saltmarsh is reached in respectively week 23, 23, 30 and 23.

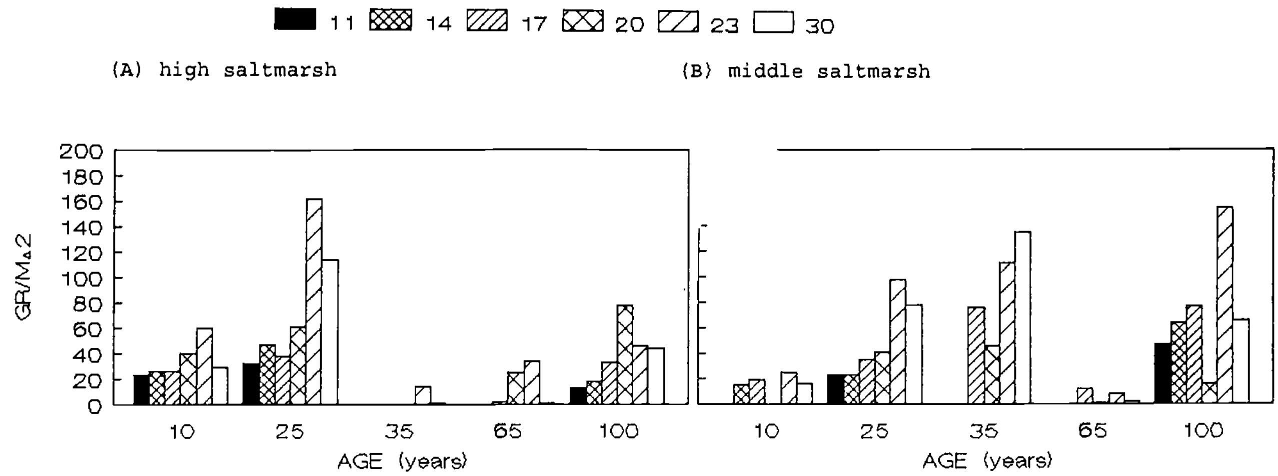

Figure 11. The *Festuca rubra* biomass on the (A) high and (B) middle.

The biomass increase of F. rubra (Figure 12) increases significantly during succession on the middle and high saltmarsh. The values of the 35 high and 35 and 65 middle saltmarsh are not shown, because the regression was not significant.

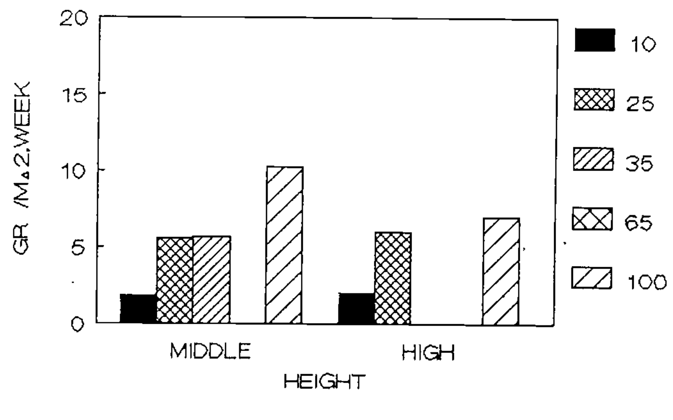

Figure 12. The biomass increase of *Festuca rubra* on the middle and high saltmarsh.

The biomass of *Pu. maritima* (Figure 13) increases and the peak biomass on the 10 (59.64 gr/m² ± SE 13.31), 25 (9.18 gr/m² ± SE 4.14) and 100 (43.13 gr/m² ± SE 10.81) years low saltmarsh is reached at respectively week 20, 20 and 23. The biomass of *Pu. maritima* on 35 and 65 years low saltmarsh is very small. On the 10 years middle saltmarsh, the biomass of *Pu. maritima* is almost constant during spring (21.06 gr/m² ± SE 4.87). Only *Pu. maritima* is found on the 25 years middle (23.25 gr/m² ± SE 10.70) and high (20.00 gr/m² ± SE 11.78) saltmarsh in week 20. No significant biomass-increases *Puccinellia maritima* are found.

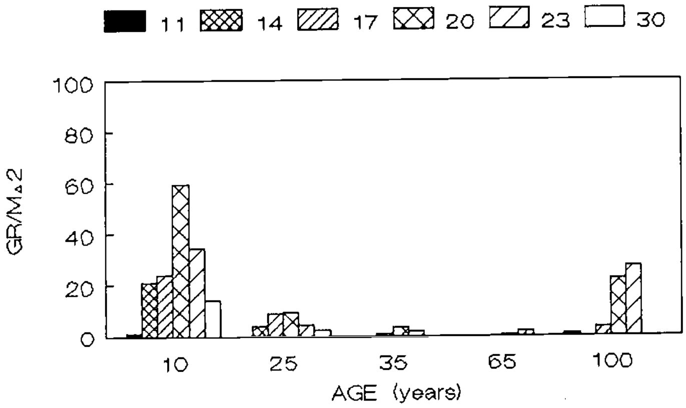

Figure 13. The *Puccinellia maritima* biomass on the low saltmarsh.

On the low, middle and high saltmarshes dead material (Figure 14) increases significantly during succession (resp. low: r=0.35 p<0.001 n=99; middle: r=0.47 p<0.001 n=100; and high: r=0.75 p<0.001 n=100). It seems that accumulation of dead material reaches a maximum after 65 years of succession on the low and middle saltmarsh. The mean biomass of dead material of 65 years low and middle saltmarsh (resp. 289.6 gr/m² ± SE 54.2 and 265.1 gr/m² ± SE 37.9) and 100 years low and middle saltmarsh (resp. 241.8 gr/m² ± SE 41.6 and 262.8 gr/m² ± SE 21.1) did not differ significantly (within each height) (ONEWAY-SNK, p>0.05). On the high saltmarsh, dead material increase strongly after 35 years of succession. The dead biomass on the 65 and 100 years old high saltmarsh (resp. 635.3 gr/m² ± SE 55.0 and 584.4 gr/m² ± SE 56.2) is significantly higher than the 10, 25 and 35 years old high saltmarshes (resp. 57.8 gr/m² ± SE 10.0, 134.4 gr/m² ± SE 26.0 and 240.8 gr/m² ± SE 14.8)(ONEWAY-SNK, p<0.05).

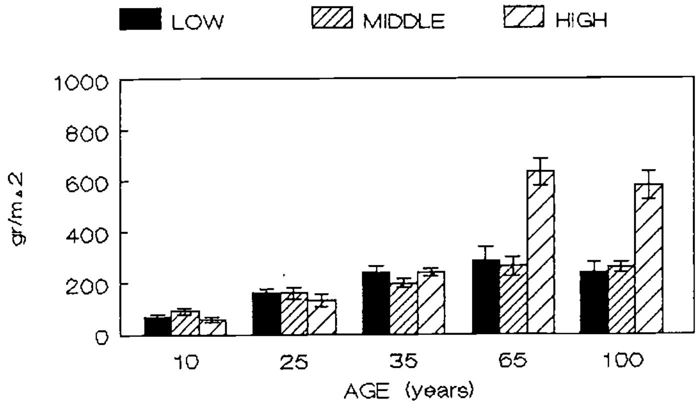

Figure 14. The mean dead biomass (period 17 until 30) on the low, middle and high saltmarsh.

The productivity rate or the biomass-increase (Figure 15) during succession increases significantly until the 65 years of succession on the old middle and high saltmarsh. The biomass-increase on the 100 years old middle and high saltmarsh seems smaller than on the 65 years old middle and high saltmarsh. The data of 35 and 65 year old low saltmarsh are not shown, because the regression was not significant (resp. p=0.37 and p=0.20). The highest productivity rate is reached at 65 year old middle and high saltmarsh.

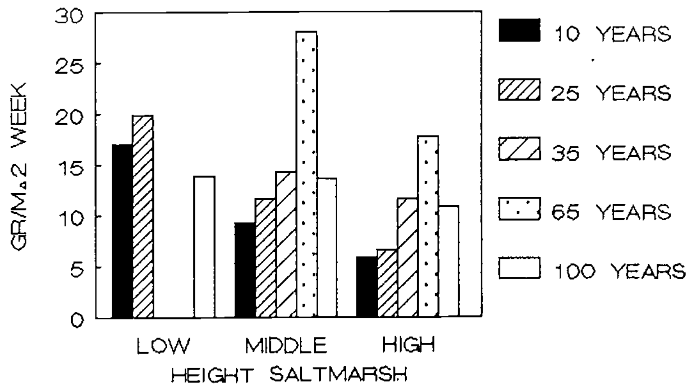

Figure 15. The biomass increase on the low, middle and high saltmarsh.

Nitrogen concentration of fresh and dead material, *Festuca rubra* and *Puccinellia maritima*.

The nitrogen concentration of fresh material (NCFM) (Figure 16) increases during the first two sample periods. After week 17 the nitrogen concentration of fresh material tends to decrease. The decrease of NCFM (Figure 17) on the low and middle saltmarsh remains constant during succession. On the high saltmarsh, the decrease of NCFM increases during succession. When pooling the transects, there are no significant differences between the three zonations (ONEWAY-SNK, P>0.05).

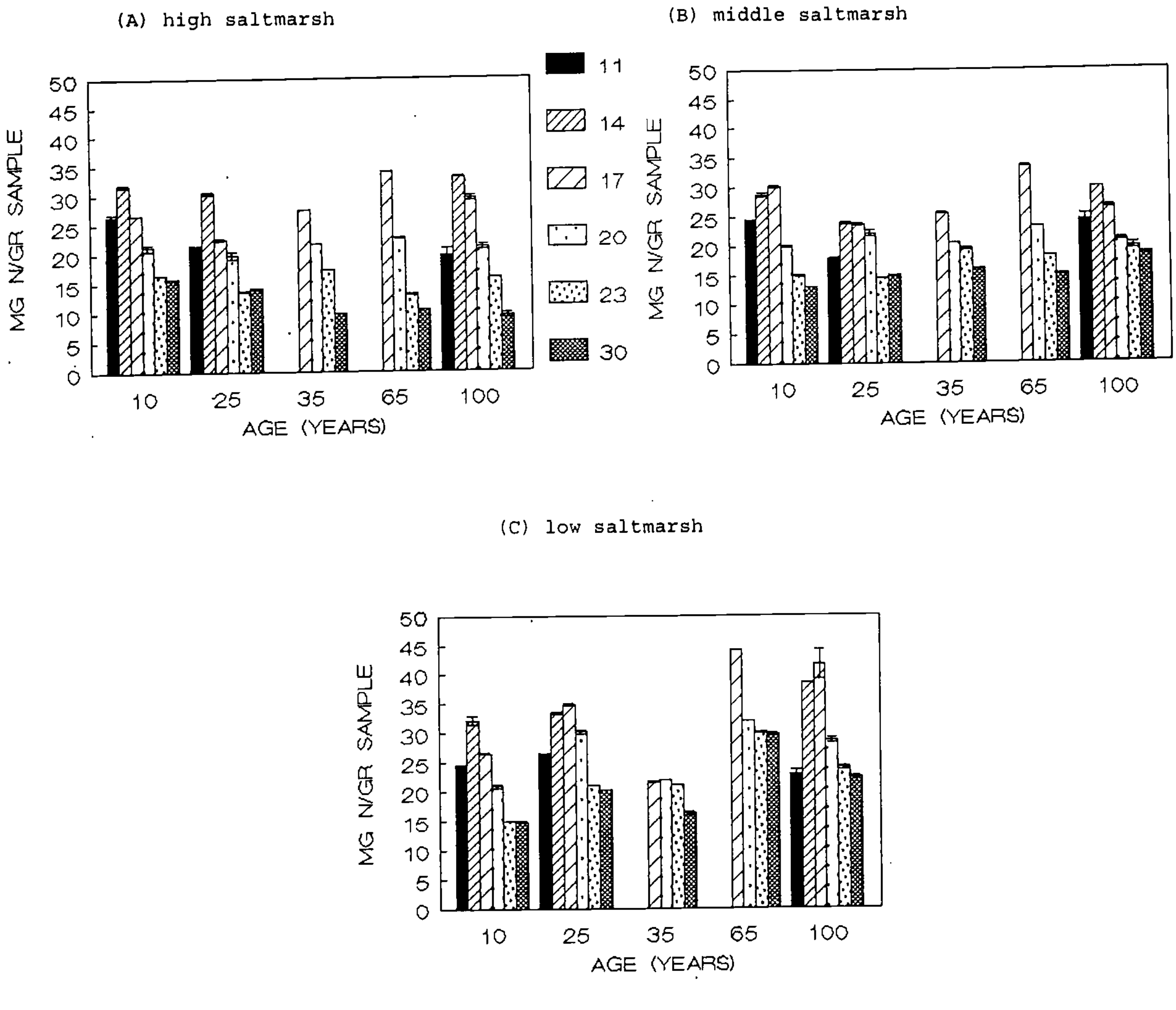

Figure 16. The nitrogen concentration of fresh material on the (A) high, (B) middle and (C) low saltmarsh.

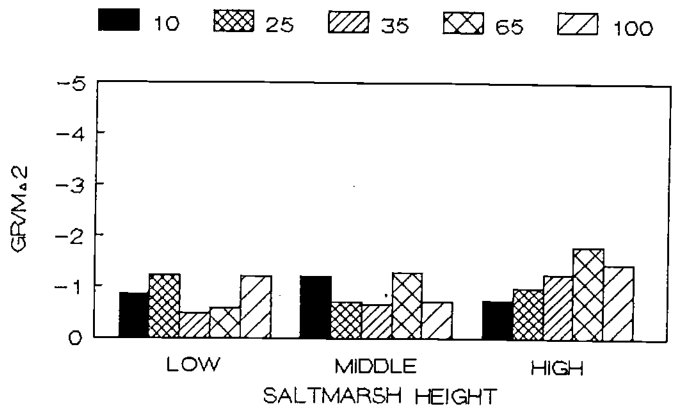

Figure 17. The decrease of the nitrogen concentration of fresh material on the low, middle and high saltmarsh.

In Figure 18, the mean *F. rubra* nitrogen concentration (week 17 until week 30) of the high saltmarsh (18.68 mg/gr ± SE 1.19) is higher than the middle saltmarsh (20.02 mg/gr ± SE 1.32), but does not differ significantly. The nitrogen concentration of *F. rubra* decreases significantly after the peak nitrogen concentration in week 14 on the middle and high saltmarsh (resp. $y_{middle}=-0.832x + 39.05$, $r=0.75$, $p<0.001$ and $y_{high}=-1.101x + 43.90$, $r=0.90$, $p<0.001$).
The nitrogen concentration of *F. rubra* in period 1 and 2 on the high and middle saltmarsh is significantly higher than in period 3 (Table 2).

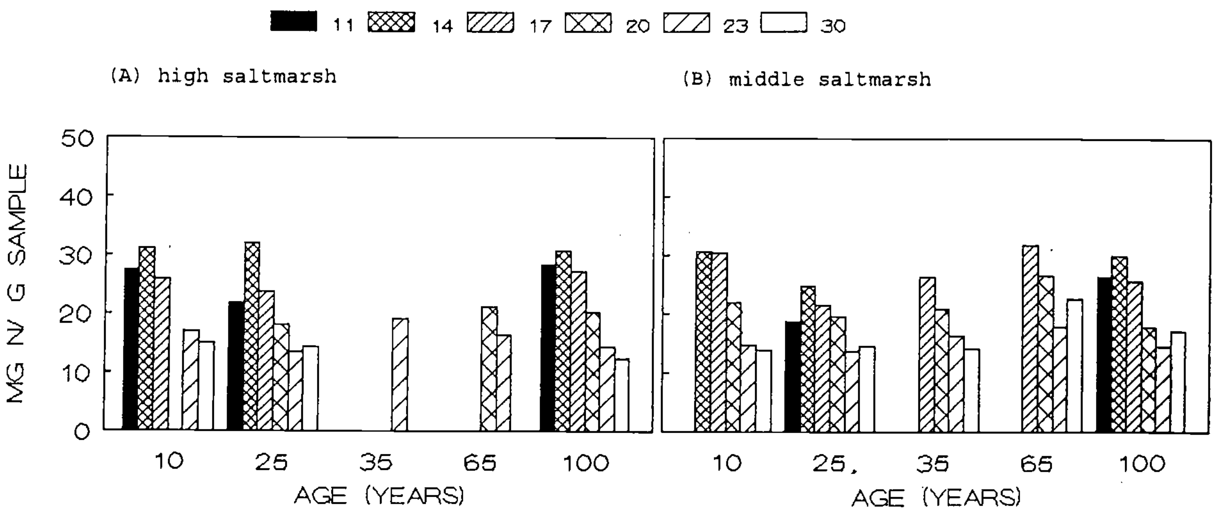

Figure 18. The *Festuca rubra* nitrogen concentration of the (A) high and (B) middle saltmarsh.

Table 2. The nitrogen concentration of *Festuca rubra* pooled per period per zonation (ONEWAY-SNK, $p<0.05$).

SALTMARSH	PERIOD	mg N/gr SAMPLE (SE)	SIGN.
HIGH	1	28.52 (1.55)	a
	2	25.58 (1.04)	a
	3	17.96 (0.98)	b
MIDDLE	1	26.11 (2.18)	a
	2	27.14 (1.80)	a
	3	18.04 (1.33)	b

The nitrogen concentration of *Pu. maritima* (Figure 19) decreases after the first sample period in week 14 on the 10 and 25 years low saltmarsh. The mean *Pu. maritima* nitrogen concentration on the low saltmarsh (22.78 mg/gr ± SE 1.84) is not significantly higher than on the middle saltmarsh (20.38 mg/gr ± SE 1.96).

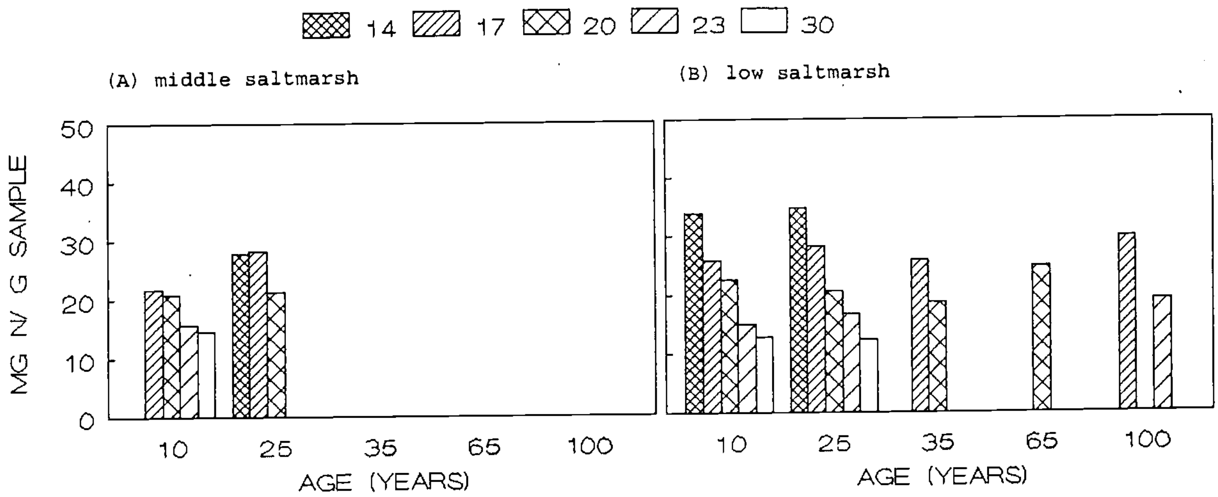

Figure 19. The *Pu. maritima* nitrogen concentration of the (A) middle and (B) low saltmarsh.

The nitrogen concentration of *Pu. maritima* in period 1 is significantly higher than in period 2, which is significantly higher than in period 3 (Table 3).

The mean nitrogen concentration of dead material is shown in Figure 20. The mean nitrogen concentration of dead material of all the low saltmarshes together has a significant higher nitrogen concentration (ONEWAY-SNK, $p<0.05$) than the middle and high saltmarsh. On the low saltmarsh, the dead material of the 65 year old saltmarsh has the highest nitrogen concentration (ONEWAY-SNK, $p<0.05$).

Table 3. The nitrogen concentration of *Puccinellia maritima* pooled per period per zonation (ONEWAY-SNK, $p<0.05$).

SALTMARSH	PERIOD	mg N/gr SAMPLE (SE)	SIGN.
LOW	1	34.39 (0.52)	a
	2	27.49 (0.97)	b
	3	19.65 (1.28)	c

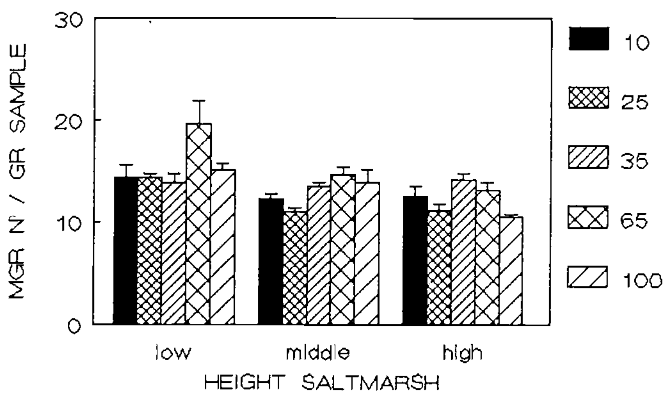

Figure 20. The mean nitrogen concentration of dead material on the low, middle and high saltmarsh.

Total nitrogen in fresh material, *Festuca rubra*, *Puccinellia maritima* and dead material.

The total nitrogen in fresh material (Figure 21) does significantly increase on the low and middle saltmarsh (like the biomass) during the growing season. On the high saltmarsh, the total nitrogen in fresh material is nearly constant within the transects during the growing season.

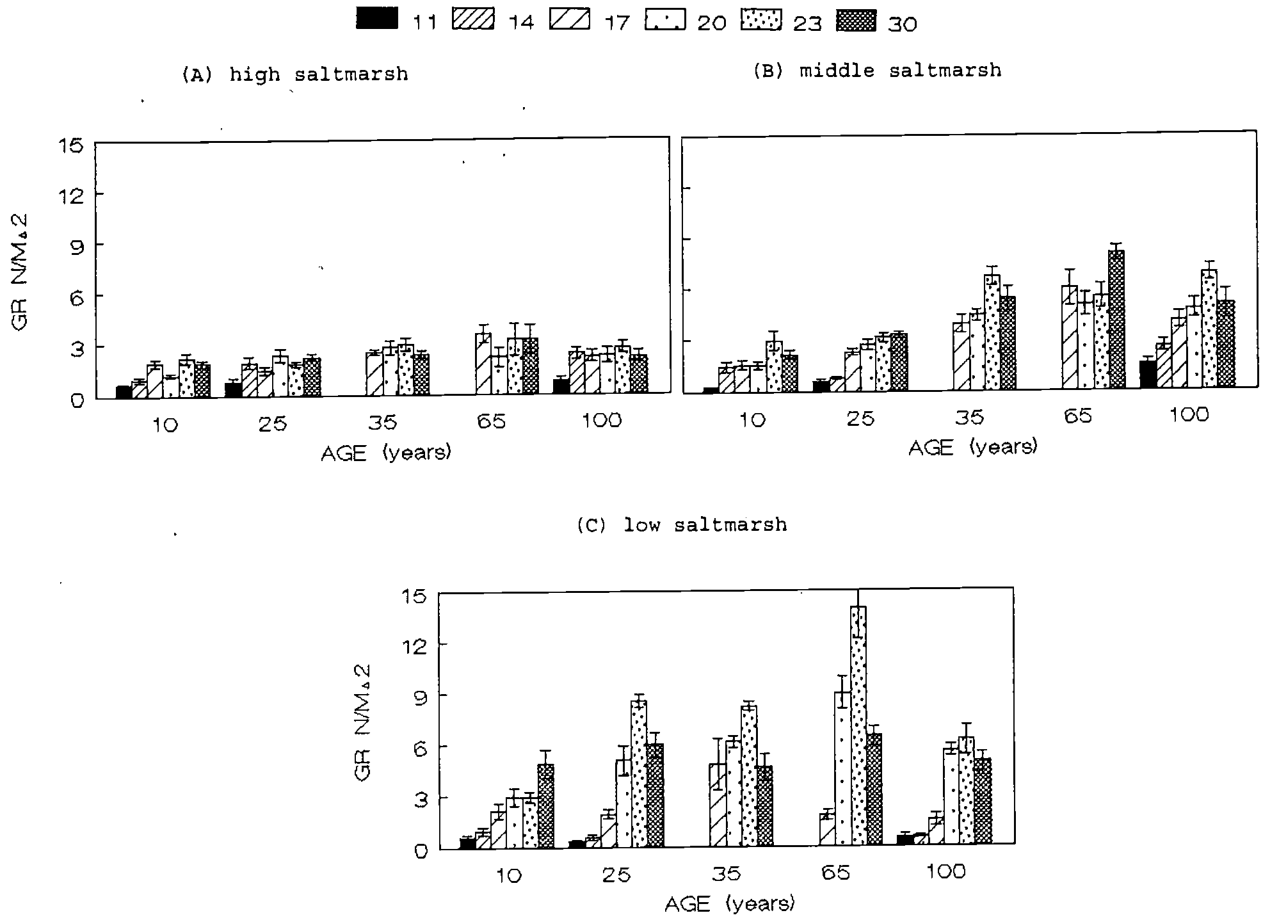

Figure 21. The total nitrogen in fresh material on the (A) high, (B) middle and (C) low saltmarsh.

The total amount of *F. rubra* nitrogen biomass (Figure 22) on the 10 years middle and high saltmarsh remains constant and increases on the 25 and 100 years middle and high saltmarsh. On the 100 years middle and high saltmarsh, the peak *F. rubra*-nitrogen biomass is reached in week 20. The *F. rubra*-nitrogen biomasses on the 65 years middle and high saltmarsh and on the 35 high saltmarsh are very small. On the 35 years middle saltmarsh, the *F. rubra*-nitrogen biomass is relatively high, but remains constant during spring.

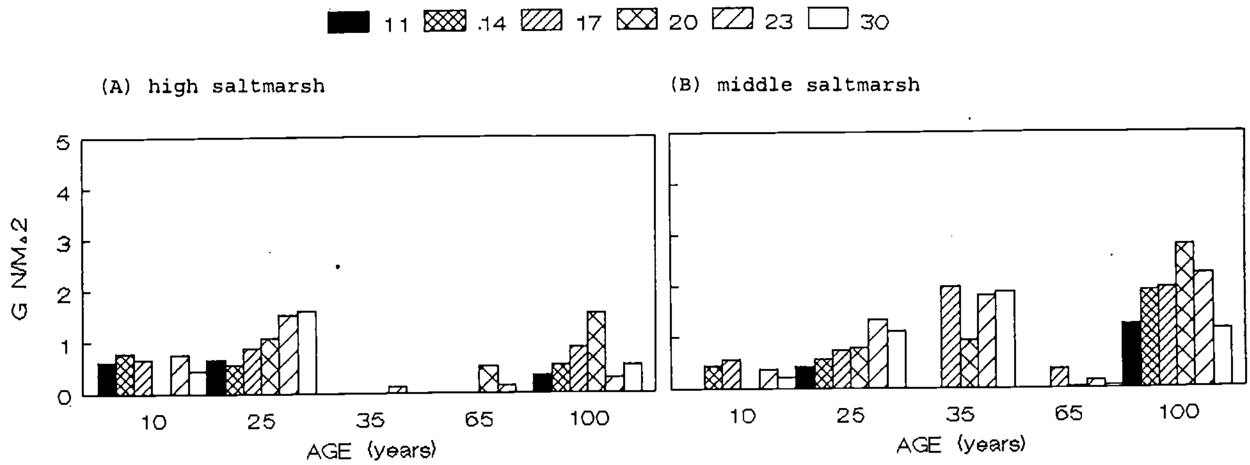

Figure 22. The total amount of *F. rubra* nitrogen biomass on the (A) high and (B) middle saltmarsh.

The *Pu. maritima* nitrogen biomass (Figure 23) increases on the 10 years low saltmarsh until a peak is reached in week 30. On the 10 years middle saltmarsh, the *Pu. maritima* nitrogen biomass remains almost constant.

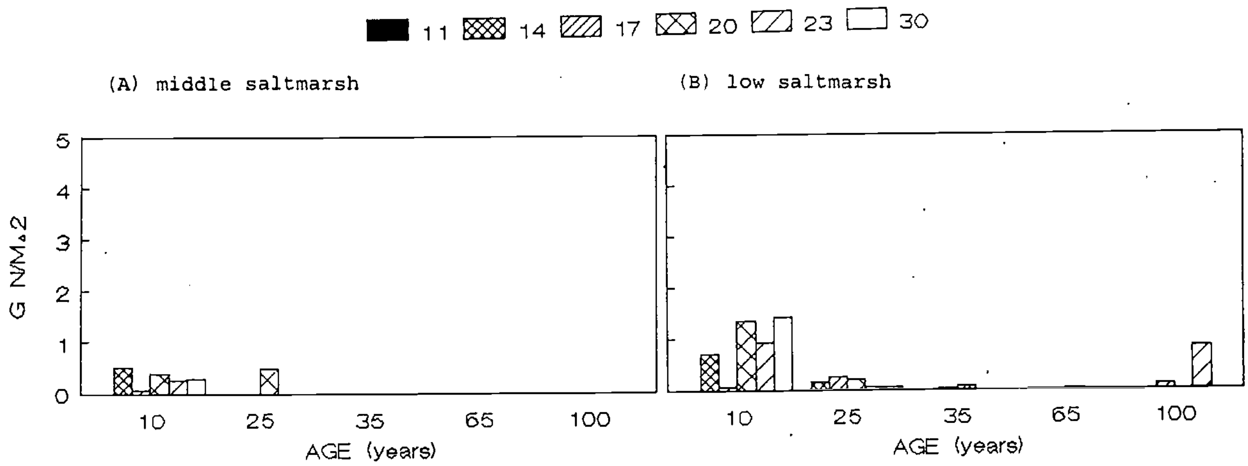

Figure 23. The total amount of *Pu. maritima* nitrogen biomass on the (A) middle and (B) low saltmarsh.

The total amount of nitrogen in dead material increases (Figure 24) significantly in the low, middle and high saltmarsh until a maximum is reached at 65 years, respectively $r_{low}=0.62$ $p<0.001$ $y=0.08x+0.28$; $r_{middle}=0.58$ $p<0.001$ $y=0.05x+0.71$; $r_{high}=0.84$ $p<0.001$ $y=0.15x-1.38$. The total amount of nitrogen in dead material is on the 65 years old low and high saltmarsh is significantly highest.

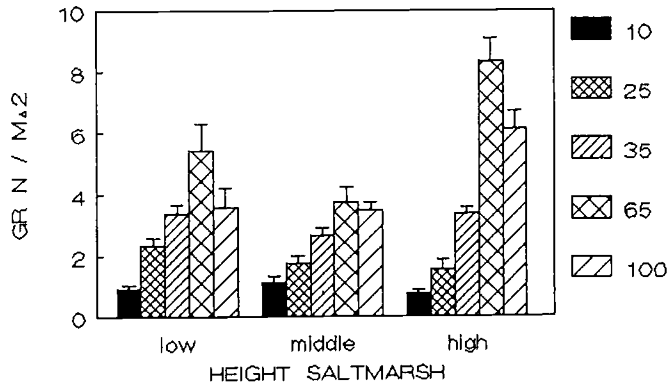

Figure 24. The total amount of nitrogen in dead material on the low, middle and high saltmarsh.

Herbivores in saltmarsh succession.

The Barnacle geese start foraging on the saltmarsh in the beginning of March. The Barnacle and Brent geese are leaving to their breeding grounds (Figure 25) at respectively April (week 15 and 16) and in the end of May (week 21 and 22).

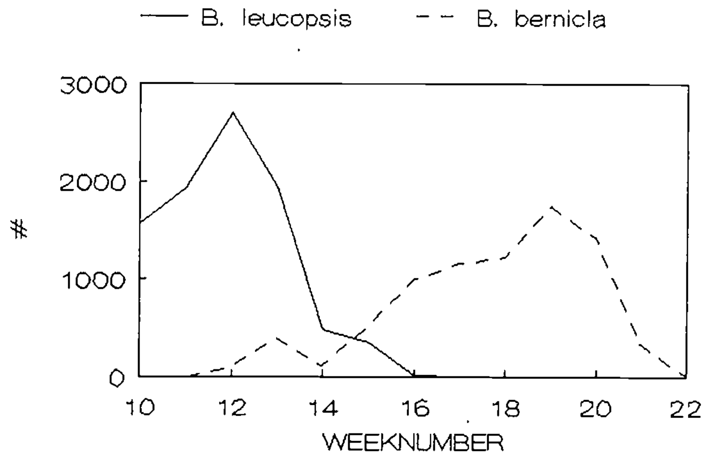

Figure 25. Counts of geese flocks on the saltmarsh of Schiermonnikoog during fieldwork.

The time when geese use the saltmarsh, can be divided into three periods (1-3). In the first period, mainly Barnacle Geese use the saltmarsh. The Brent Geese are the only goose species left in the third period. In the second period, both geese are on the island.

The grazing pressure of the three zonations is shown in Table 4. The grazing pressure on the high saltmarsh decreases in spring. In period 3, the grazing pressure on the middle saltmarsh is significantly lower than in period 1 and 2. The grazing pressure on the low saltmarsh in period 1 is significantly lower than in period 2 (which is significantly higher than period 3) and 3.
The grazing within the periods is shown in Table 5. The grazing pressure in period 1 on the middle and high saltmarsh is significantly higher than on the low saltmarsh. No significant differences in grazing pressure between the high, middle and low saltmarsh are found in period 2, when both geese are spring staging on the island. In period 3, a significantly higher grazing pressure is found on the low and middle saltmarsh than on the high saltmarsh. The grazing pressure on the low saltmarsh is significantly higher than on the middle saltmarsh.

Table 4. Grazing pressure within the saltmarsh height. The character gives significant differences (ONEWAY SNK, $p<0.05$).

SALTMARSH	PERIOD	DROP/M²WEEK (SE)	SIGN.
HIGH	1	0.89 (0.080)	a
	2	0.65 (0.113)	b
	3	0.09 (0.045)	c
MIDDLE	1	0.98 (0.087)	a
	2	1.01 (0.140)	a
	3	0.40 (0.089)	b
LOW	1	0.36 (0.048)	a
	2	0.89 (0.109)	b
	3	0.61 (0.078)	c

The general pattern of geese foraging on the three zonations is now known. Barnacle and Brent geese forage respectively on the high and middle saltmarsh and on the middle and low saltmarsh. In Figure 26 is shown where the geese forage in the succession. In general, the grazing pressure is low on the whole 100 years old saltmarsh. In period 1, the grazing pressure is constant on the 10 until 65 years old high saltmarsh. The 35 and 65 years old middle and the 25 and 65 years old low saltmarsh have the highest grazing pressure (ONEWAY-SNK, $p<0.05$). In period 2, the grazing pressure on the 10, 35 and 65 years old high saltmarsh is significant the highest (ONEWAY-SNK, $p<0.05$). The grazing pressure of the 65 years old middle saltmarsh is significantly higher than the 25 years old middle saltmarsh (ONEWAY-SNK, $p<0.05$). The grazing pressure of the 25 years old low saltmarsh is significantly higher than the 10, 35 and 65 years old low saltmarsh (ONEWAY-SNK, $p<0.05$). In period 3, only the 25 years old high saltmarsh is visited. The grazing pressure on the 25 years old middle and low saltmarsh is significantly higher than the 10 years old middle and low saltmarsh (ONEWAY-SNK, $p<0.05$).

Table 5. Grazing pressure within period 1-3. The character gives significant differences (ONEWAY SNK, $p<0.05$).

PERIOD	SALTMARSH	DROP/M^2WEEK (SE)	SIGN.
1	LOW	0.36 (0.048)	a
	MIDDLE	0.98 (0.087)	b
	HIGH	0.89 (0.080)	b
2	LOW	0.89 (0.109)	a
	MIDDLE	1.01 (0.140)	a
	HIGH	0.65 (0.113)	a
3	LOW	0.61 (0.078)	a
	MIDDLE	0.40 (0.089)	b
	HIGH	0.09 (0.045)	c

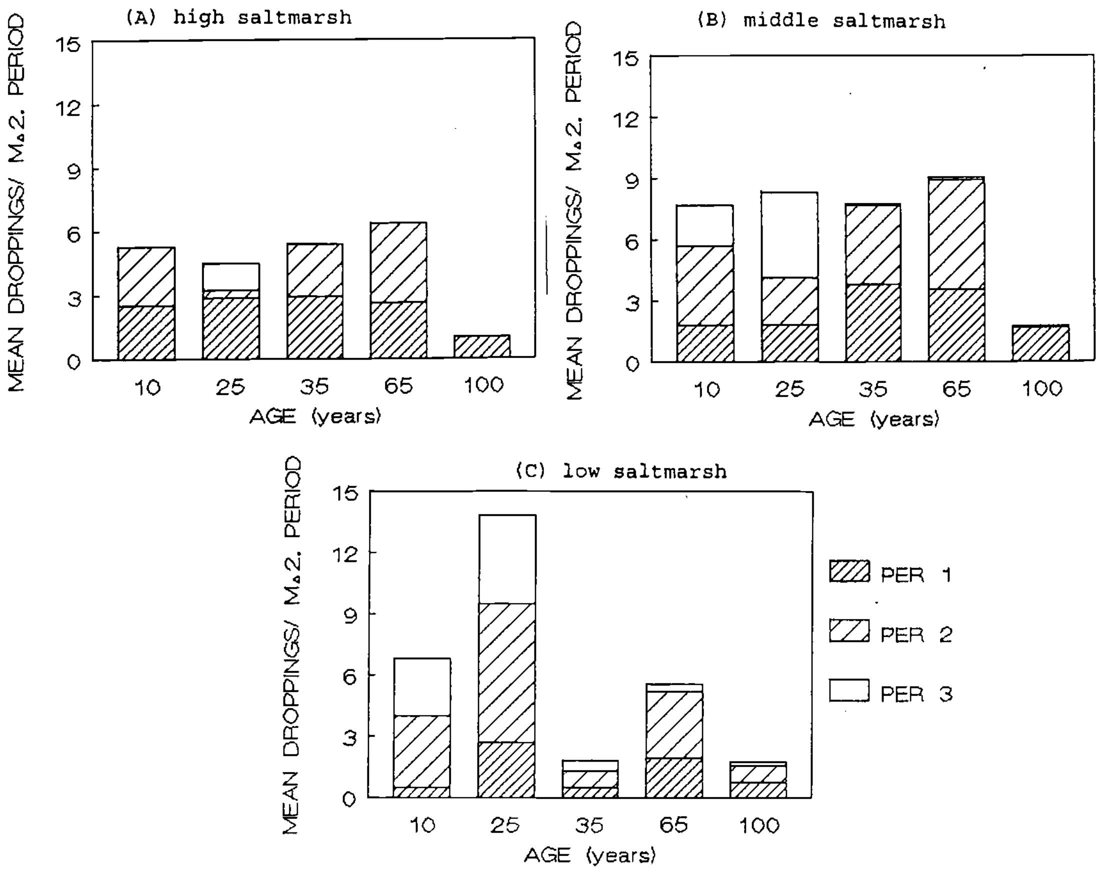

Figure 26. Grazing pressure on the (A) high, (B) middle and (C) low saltmarsh of Schiermonnikoog in three periods.

DISCUSSION.

Vegetation succession.

Terrestrial plant succession is defined as the dynamics of plant populations on an initially bare substrate (Tilman 1988). At the start of primary succession, according to Tilman (1988), the habitat experienced by the seedlings of new colonists has low nutrient but high light availability. As various soil-forming processes, mediated by numerous decomposer species, increase the availability of the limiting soil resource(s), total plant biomass increases (Figure 9) and light penetration to the soil surface decreases (Figure 8). Thus, primary successions, at least during their first few hundred years, can be thought of as a gradient through time in the relative availability of one or more limiting soil resources and light at the soil surface.

At the earliest stage of saltmarsh succession at Schiermonnikoog, the soil N pool size was low, as in most of the parent material in which soils are formed (Olff *et al.* 1992, Crocker & Major 1955, Jenny 1980). Olff *et al.* (1992) showed that N pool size increases with an increasing claylayer thickness (43 g m^{-2} with every mm of clay). The amount of nitrogen released during nitrogen mineralisation increases during succession, but the young saltmarsh mineralizes procentually more nitrogen (Bakker *et al.* 1993).

The fresh biomass is positively correlated with the amount of nitrogen in the soil (Hazekamp & Van Hooff 1994). The peak biomass (Figure 9) and the biomass increase (Figure 15) increased during saltmarsh vegetation succession. This agrees with the findings in four Minnesota old fields by Pastor *et al.* (1987). The peak biomass and the biomass increase increases until 65 years and decreases after 65 years of succession. So, it seems that a maximum is reached at the age of 65 years of succession. Variations in peak biomass could be explained by rainfall deficit in the growing season, but not by the inundation frequency (De Leeuw *et al.* 1990). De Leeuw *et al.* (1991) also showed that the soil salinity was positively and the soil moisture content was negatively correlated with the rainfall deficit in a two-year period in these mid and high saltmarsh communities. Hazekamp & Van Hooff showed that the soil moisture content increases with increasing thickness of the clay-layer. The production of lower saltmarsh ecosystems, in contrast, is probably not affected by the rainfall deficit during the growing season (de

Leeuw *et al.* 1991).

The percentage fresh material decreases and the total dead biomass increases during succession. This means an accumulation of dead material during succession until 65 years of succession and a maximum is reached at 65 years. The slow accumulation of dead material on the low and middle saltmarsh might be attributed to the influence of inundations. The low and middle saltmarshes are more often inundated than the high saltmarsh (Bakker 1989). This might explain the significant higher nitrogen concentration of dead material on the low saltmarsh. On the dead material of the low saltmarsh might be some clay left, because the vegetation is not washed. The strong accumulation of dead material on the 65 and 100 years high saltmarsh can be attributed to *Elymus athericus* (Figure 7). *Elymus athericus* becomes the dominant on the high saltmarsh, where it initially only was found on the highest parts (Olff *et al.* 1992). This increase of *Elymus athericus* can be attributed to an increase of the nutrient-pool (especially nitrogen) in the soil (Olff 1992, Van Wijnen 1993, Leendertse *et al.* 1993).
At the 65 year old saltmarsh, a maximum is reached and can be caused by two reasons. First, accumulation of dead material reduces the light availability to the soil. Competition for light between plants becomes more severe. Secondly, the input of nutrients to terrestrial systems by animals has impacts on the vegetation (Herring gulls *Larus argentus*: Sobey & Kenworthy 1979, Bazely *et al.* 1989; Red Deer *Cervus elaphus*: Iason *et al.* 1986). Bazely *et al.* (1989) found on the saltmarsh of Schiermonnikoog a significant higher nitrogen content in *Festuca rubra* in gull sites of Herring Gulls and Lesser Black-backed Gull *Larus fuscus* than in sites, where gulls are absent.

Early in the season, the nitrogen concentration is the highest (Figure 16), because the young actively growing tissues require high N levels to support rapid protein synthesis during bursts of growth. Thus, during seasonal growth cycles, peak N concentrations occur whenever the cells of a plant tissue or organ are rapidly expanding in number and size (Mattson 1980). This could explain the general decrease of the nitrogen concentration on the low, middle and high saltmarsh. The decreasing nitrogen concentration on the high saltmarsh can be explained that lightcompetiting plant species invest in stem elongation, this will lead to a lowering of the nitrogen concentration in the plant (Mattson 1980). The distribution of total nitrogen in the vegetation resembles the distribution of the biomass. The amount of nitrogen in the fresh biomass is negatively correlated with the amount of nitrogen in the soil (Hazekamp & Van Hooff 1994).

The salinity of the soil moisture increases from the high to the low saltmarsh during succession (Hazekamp & Van Hooff 1994). Salinity has effects on the vegetation: increasing amount of roots (Jeffrey 1987), increasing nitrogen in the plant (Pigott 1969). Some studies showed that growth of saltmarsh species is nitrogen limited (*Suaeda maritima* (Pigott (1969), Stewart *et al.* (1972), *Salicornia* spec. (Pigott (1969)). Pigott (1969) showed that large lower-saltmarsh plants had higher nitrogen concentrations than the small plants from the upper-saltmarsh plant.

Geese and succession.

Barnacle geese.

Barnacle Geese are present on Schiermonnikoog from November until April. Prins & Ydenberg (1985) showed that in late February or early March, the Barnacle geese shift from the polder to the saltmarsh. This abrupt switch in foraging terrain by Barnacle geese takes place when crude protein and mineral content of *F. rubra* are equal in both the polder and the saltmarsh (Prins & Ydenberg 1985). A high level of disturbance in the polder (Owen 1980) and the quality and digestion of food (Lichtenbelt 1981) might explain this.

From the abrupt switch to the saltmarsh until mid-April, the number of Barnacle geese staying on the island increases until approximately 6500. The bodymass of the geese increases, because reserves are built up. Around mid-April (week 14 and 15) the geese migrate to their breeding grounds on Novaya Zemlya (Figure 25). In Barnacle Geese individuals ranking lowest in condition at the moment of departure to the breeding grounds failed to incubate successfully (Prop & Nugent, unpublished), but a large amount of body reserves is no guarantee of successful reproduction, nevertheless it is probably a prerequisite (De Boer & Drent 1989).

The Barnacle geese forage mainly on the (25 - 65 years) high and middle saltmarsh (Figure 26). Remarkable is the low coverage and biomass of *F. rubra* (Figure 3 and 11) on the 35 and 65 high and 65 middle saltmarsh. In the field, small holes (probably made by Barnacle geese) in the vegetation were found, which might be used by Barnacle geese to forage on palatable seedlings covered by the vegetation or rhizomes of *F. rubra* (Smit & Van der Wal, pers. comm.).

On the saltmarsh, the Barnacle Geese mainly forage on *F. rubra* (90%), based on epidermal analysis of faeces (Ydenberg & Prins 1981). Ydenberg & Prins (1981) showed that high levels of protein in *F. rubra* were a direct effect of repeated grazing by Barnacle geese. Input of nutrients by animals can increase the N-quality of plants. Barnacle geese spent significantly more time grazing in sites with evidence of Herring Gull *Larus argentatus* and Lesser Black-gull *L. fuscus* breeding activity than in nearby non-gull sites (Bazely *et al.* 1989). They found a significant higher nitrogen content of *F. rubra* in gull sites. These colonies are located at the higher saltmarsh (35 and 65 years) dominated by *F. rubra* and *Elymus athericus* (own observation). Fertilizing effects of geese droppings are reported in several publications (Balkenhol *et al.* 1984, Cargil & Jefferies 1984, Bazely & Jefferies 1985, Madsen 1989).

Brent geese.

The major part of the world population of the Dark-bellied Brent Geese *Branta bernicla bernicla* is concentrated in the Waddensea (Ebbinge et al. 1981, Prokosch 1984). From November until April the Brent Geese forage in the polder. The numbers of Brent geese (Figure 25) increased from mid-April (week 15) and primarily forage on the saltmarshes. The departure of Brent geese takes place respectively in week 20 and 21 (Figure 25) to the breeding grounds on the Taymir-Peninsula. On Schiermonnikoog during April and May, the Brent Geese increase about 33% of their bodymass and variation in breeding success of Brent Geese in the arctic could be partially explained by their body weight at the end of spring staging (Ebbinge 1992).

The Brent geese forage mainly on the 10, 25 and 35 years middle and low saltmarsh in the second half of April and May (Figure 26). *E. athericus* becomes dominant at the high saltmarsh during succession (Figure 7). Olff *et al.* (1992) showed that Brent geese did not graze in areas where this grass species was dominant and were therefore probably restricted to the early successional stages. The four plant species of interest for the geese occur in these early successional stages (Figure 3 - 6).

Prop & Deerenberg (1991) showed that the large increase of bodymass is only possible through very selective foraging on only few plant species. The staple food is *Puccinellia maritima* and later *Festuca rubra* (when the production of the first dropped) and is supplemented with *Plantago maritima* and

Triglochin maritima. The importance of *Puccinellia maritima* (having a high quality) decreases during the spring, because the metabolizable energy of this plant declines. Although *Plantago maritima* and *Triglochin maritima* are less commonly taken, they appear to be the most profitable plants to eat. The proportion of these species in the diet is restricted by (1) the capacity of the alimentary tract and (2) the limited distribution of these plants, in combination with their rapid depletion by grazing geese. Prins *et al*. (1980) showed that Brent Geese foraging on *Plantago maritima* regraze the same plant every four days. Every time 30% of the rosette is grazed and this regime of harvesting gives the highest regrowth of new plant tissue. Selection of foraging area and the important plant species is crucial for the geese.

Geese leaving to their arctic breeding grounds.

During the whole spring, geese are on the island and both geese (Barnacle and Brent) leave to their breeding grounds in the high arctic (resp. Novaya Zemlya and Taymir-peninsula) resp. in mid-April and the end of May. The distance to the breeding grounds for Barnacle geese is ± 3400 km and for Brent geese ± 4300 km. It appears that Brent geese and possibly also Barnacle geese take their trip to their breeding grounds in steps. This means that both geese deposit again body reserves at these stopover sites.

The feeding conditions in spring differ between the goose species. The Barnacle geese forage on *F. rubra*, which is the staple food (Ydenberg & Prins 1981), on the high and middle saltmarsh (Figure 26 and Table 5). High levels of nitrogen of F. rubra are a direct result of repeated grazing (Ydenberg & Prins 1981). The Brent geese forage on the middle and low saltmarsh (Figure 26 and Table 5) mainly on *Pu. maritima* and *F. rubra*, when production of the first one dropped, while *Pl. maritima* and *T. maritima* were less commonly taken (Prop & Deerenberg 1991). During spring the nitrogen concentration (Figure 18 and 19) and metabolizable energy of *F. rubra* declines (Prop & Deerenberg 1991). The gross intake rate (GIR) of *T. maritima* and *Pl. maritima* increases, while the GIR of *F. rubra* and *Pu. maritima* remains constant (Prop & Deerenberg 1991). The Brent geese regraze *Pl. maritima* every four days, which gives the highest regrowth (Prins *et al*. 1980)

Thus, the Barnacle geese have to forage on *F. rubra* during their stay on the saltmarsh, because it is the most abundant food plant having a high nitrogen concentration. The

Brent geese have to cope with a situation, in which the nitrogen concentration of *F. rubra* declines rapidly. The diet of Brent geese should be extended in order to deposit the same reserves. So, the diet is supplemented with *Pl. maritima* and *T. maritima*.

CONCLUSION.

Olff *et al.* (1993) showed an increase of nitrogen in the soil. The soil coverage decreases during vegetation succession (Figure 8) and thus the vegetation coverage increases. The productivity increases during vegetation succession (Figure 15). A maximal productivity (Figure 15) and peak standing crop (Figure 9) is reached after 65 years of succession. The amount of dead material increases during succession, especially on the high saltmarsh (Figure 14).

The Barnacle geese forage on the high and middle saltmarsh between 25 and 65 years of succession. The feeding conditions on the high (and middle) saltmarsh are decreasing during spring (death material accumulates (Figure 14), *Elymus athericus* increases (Figure 7), nitrogen concentration of *Festuca rubra* decreases (Table 2)).

The Brent geese forage on the middle and low saltmarsh between 10 and 35 years of succession. In May, the Brent geese forage mainly on *Pu. maritima* on the low saltmarsh. The quality (or nitrogen concentration) of *Pu. maritima* is significantly smaller in May (Table 3). Therefore, the diet is supplemented with high nutritious feeding plants (*Plantago maritima* and *Triglochin maritima*)

LITERATURE.

Balkenhol, B., H.H. Bergmann, R. Holländer & M. Stock (1984). Über den EinfluB von Gänsekot auf die Vegetation von Grünflächen. Okol. Vögel 6: 223-247.

Bakker, J.P. (1989). Nature management by cutting and grazing. Junk, Dordrecht.

Bakker, J.P., H. Olff, M. Loonen, A. Hazekamp, E. van Hooff & R. Kats (1994). Plant Species Composition, Plant Production, Compartmentation of Nitrogen and Geese Grazing in a Successional Gradient on Saltmarshes. In: Long-term vegetation changes in relation to wild herbivores in coastal ecosystems. Acta Bot. Neerl. 43 (2): 217.

Bazely, D.R. & R.L. Jefferies (1985). Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. Journal of Applied Ecology 22: 693-703.

Bazely, D.R., P.J. Ewins & R.H. McCleery (1989). Possible effects of local enrichment by gulls on feeding-site selection by wintering Barnacle Geese *Branta leucopsis*. Ibis 133: 111-114.

Bell, R.H.V. (1970). The use of herb layer by grazing ungulates in the Serengeti. In A. Watson (ed.): *Animal Populations in Relation to Their Food Resources*, pp. 111-124. Blackwell Scientific Publications, Oxford.

Berendse, F. (1990). Organic matter accumulation and nitrogen mineralization during secondary succession in heathland ecosystems. Journal of Ecology 78: 413-427.

Boudewijn, T. (1984). The role of digestibility in the selection of spring feeding sites by Brent Geese. Wildfowl 35: 97-115.

Cargil, S.M. & R.L. Jefferies (1984). The effects of grazing by Lesser Snow Geese on the vegetation of a subarctic saltmarsh. Journal of Applied Ecology 21: 669-686.

Chapman, V.J. (1974). Saltmarshes and salt deserts of the world. Cramer, Lehre, 2nd ed.

Crocker, R.L. & J. Major (1955). Soil development in relation to vegetation and surface age at Glacier Bay. Journal of Ecology 43: 427-448.

Davies, J.C. & F. Cooke (1983). Annual nesting and productivity in Snow Geese: prairie droughts and arctic nesting. J. Wildl. Manage. 47: 291-296.

DeAngelis, D.L. (1992). Dynamics of nutrient cycling and foodwebs. Chapman & Hall, London.

De Boer, W.F. & R.H. Drent (1989). A matter of eating or being

eaten? The breeding performance of arctic geese and its implications for waders. Wader Study Group Bull. 55: 11-17.
De Leeuw, J., H. Olff & J.P. Bakker (1990). Year-to-year variation in peak aboveground biomass of six saltmarsh angiosperm communities as related to rainfall deficit and inundation frequency. Aquatic Botany 36: 139-151.
De Leeuw, J., A. van den Dool, W. de Munck, J. Nieuwenhuize & W.G. Beeftink (1991). Factors influencing the soil salinity regime along an intertidal gradient. Estuarine, Coastal and Shelf Science 32: 87-97.
De Leeuw, J., W. De Munck, H. Olff & J.P. Bakker (1993). Does zonation reflect the succession of saltmarsh vegetation? A comparison of an estuarine and a coastal bar island marsh in The Netherlands. Acta. Bot. Neerl. 42(4): 435-445.
Ebbinge, B., M. Fog & P. Prokosch (1981). Brent Goose (*Branta bernicla* L.). Pp. 28-37 in: C.J. Smit & W.J. Wolff (eds.). Birds of the Wadden Sea. Balkema, Rotterdam.
Ebbinge, B. (1992). Population limitation in arctic-breeding geese. Thesis, University of Groningen.
Hairston, N.G., F.E. Smith, L.B. Slobodkin (1960). Community structure, population control and competition. American Naturalist 94: 421-425.
Hazekamp, A. & E. van Hooff (1994). Primaire successie en stikstof mineralisatie op de kwelder van Schiermonnikoog. Doctoraal verslag. Laboratorium voor Plantenoecologie. RUG, Groningen.
Hodson, M.J., M.M. Smith, S.J. Wainwright & H. Öpik (1985). The effects of the interaction between salinity and nitrogen limitation in *Agrostis stolonifera* L. Vegetatio 61: 255-263.
Iason, G.R., C.D. Duck & T.H. Clutton-Brock (1986). Grazing and reproductive success of red deer: the effect of local enrichment by gull colonies. J. Anim. Ecol. 55: 507-515.
Jeffrey, D.W. (1987). Soil-plant relationships an ecological approach. Timber Press. USA. Portland. Pp. 235-256.
Jenny, H. (1980). Soil genesis with ecological perspectives. Ecological studies, vol. 37. New York: Springer-Verlag.
Lawrence, D.B. (1979). Primary versus secondary succession at Glacier Bay National Monument, south-eastern Alaska. In R.M. Linn (ed.): Proceedings of the first conference on scientific research in the National Parks: 213-224.
Leendertse, P., J. Rozema, G. Janssen & J. Bossinade (1993). Kwelders en waterkwaliteit; een verkenning in het waddengebied. Landschap 1993: 3-15.

Lichtenbelt, W. (1981). Research on the digestion of food by barnacle geese: the influence of daylength and the change in the composition of *Festuca rubra* during the spring. Unpublished Report, Zoological Laboratory, University of Groningen.
Madsen, J. (1989). Spring feeding ecology of Brent Geese *Branta bernicla*: annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. Dan. Rev. Game Biol. 13 (7).
Mattson, W.J. (1980). Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11: 119e MacMillian Press Ltd. London, pp. 113-126.
McLandress, M.R. & D.G. Raveling (1981). Changes in diet and body composition of Canada Geese before spring migration. Auk 98:65-79.
McNaughton, S.J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. Science 191: 92-94.
McNaughton, S.J., M. Oesterheld, D.A. Frank & K.J. Williams (1989). Ecosystem-level patterns of primary production and herbivory in terrestrial habitats. Nature 341: 142-144.
Newton, I. (1977). Timing and success of breeding in tundra-nesting geese. In Stonehouse B. Perrins (eds).: *Evolutionary ecology*. The MacMillian Press Ltd. London, pp. 113-126.
Oksanen, L., S.D. Fretwell, J. Arruda & P. Niemelä (1981). Exploitation ecosystems in gradients of primary production. American Naturalist 118: 240-261.
Olff, H., J. Huisman, & B.F. Van Tooren (1992a). Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. MS.
Olff, H., D. Tilman, M.J. Crawley & D. Wedin (1992b). Plant competition and herbivory along gradients of primary production. MS.
Owen, M. (1980). Wild geese of the world. B.T. Batsford, London.
Pastor, J., M.A. Stillwell & D. Tilman (1987). Nitrogen mineralization and nitrification in four Minnesota old fields. Oecologia 71: 481-485.
Pickett, S.T.A., S.L. Collins & J.J. Armesto (1987): A hierarchical consideration of succession. Vegetatio 69: 109-114.
Pigott, C.D. (1969). Influence of mineral nutrition on the zonation of flowering plants in coastal saltmarshes. In

I.H. Rorison (ed.),: *Ecological Aspects of the Mineral Nutrition of Plants*, pp. 25-35. Blackwell, Oxford.
Prins, H.H.Y., R.C. Ydenberg & R.H. Drent (1980). The interaction of Brent Geese *Branta bernicla* and Sea Plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neerl. 29(5/6): 585-596.
Prins, H.H.T. & R.C Ydenberg (1985). Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). Oecologia 66: 122-125.
Prokosch, P. (1984). Population, Jahrrhythmus und traditionelle Nahrungsplatzbindungen de Dunkelbäuchigen Ringelgans (*Branta b. bernicla* L. 1758) im Nordfriesischen Wattenmeer. Ökologie der Vögel 6: 1-99.
Prop, J. & C. Deerenberg (1991). Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87: 19-28.
Prop, J. & T. Vulink (1992). Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. Functional Ecology 6: 180-189.
Roozen, A.J.M. & V. Westhoff (1985). A study on long-term saltmarsh successional permanent plots. Vegetatio 61: 23-32.
Rozema, J., P. Bijwaard, G. Prast & R. Broekman (1985). Ecophysiological adaptions of coastal halophytes from foredunes and saltmarshes. Vegetatio 62: 499-521.
Sobey, D.G., & J.B. Kenworthy (1979). The relationship between herring gulls and the vegetation of their breeding colonies. J. Ecol. 67: 469-496.
Stewart, G.R., J.A. Lee & T.O. Orebamjo (1972). Nitrogen metabolism of halophytes. I. Nitrate reductase activity in *Suaeda maritima*. New Phytol. 71: 263-267.
Thomas, V.G. 1983. Spring migration: the prelude to goose reproduction and a review of its implications. In: Boyd, H. (ed.) First Western Hemisphere waterfowl and waterbird symp. Can. Wildl. Serv., Ottawa pp. 73-81.
Thomas, V.G. & J.P. Prevett (1982). The role of Horsetails (Equisetaceae) in the nutrition of Northern breeding geese. Oecologia 53: 359-363.
Tilman, D. (1985). The resource-ratio hypothesis of plant succession. American Naturalist 125: 827-852.
Tilman, D. (1985). Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton.
Valiela, I., & J.M. Teal (1974). Nutrient limitation in

saltmarsh vegetation. In R.J. Reimold & W.H. Queen (eds.): *Ecology of Halophytes*, pp. 547-563. Academic Press, New York.

Van Andel, J., J.P. Bakker & A.P. Grootjans (1993). Mechanisms of vegetation succession: a review of concepts and perspectives. Acta Bot. Neerl. 42(4): 413-433.

Vesey-Fitzgerald, D.F. (1960). Grazing succession among East African game animals. Journal of Mammalogy 41: 161.(uit Ydenberg&prins 1981)

Westhoff, V. (1979): Phytosociology in the Netherlands: history, present state, future. In Werger, M.J.A. (ed): *The Study of Vegetation*, 83-121. Junk Publicers, Den Haag.

Wijnen, H. van (1993). Primaire successie op de kwelder in relatie tot stikstof in de bodem. Doctoraal verslag. Laboratorium voor plantenoecologie. RUG. Groningen.

Wypkema, R.C.P. & C.D. Ankney (1979). Nutrient reserve dynamics of lesser snow geese staging at James Bay, Ontario. Can. J. of Zoology 57: 213-219.

Ydenberg, R.C. & H.H.T. Prins (1981). Spring grazing and the manipulation of food quality by Barnacle Geese. Journal of Applied Ecology 18: 443-453.