

# **The impact of goose foraging on**

## *Spartina anglica*

### **Plant performance under field- and laboratory conditions**

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April 1998

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## SUMMARY

Since 1991, Greylag Geese use the island of Schiermonnikoog as an autumn and winter staging area. In the season of 1995-1996, approximately 700 Greylags wintered on the island. The Greylags were mainly found in two areas. A brackish *Scirpus maritimus* marsh served both as roosting- and foraging area. The salt marsh served as a day-time foraging area. In the salt marsh, Greylags foraged on the below-ground parts of *Spartina anglica*. In contrast to *Scirpus maritimus*, goose foraging on below-ground parts of *Spartina anglica* has only rarely been described. The effects of goose grubbing on *Spartina anglica*, a relatively new species, are largely unknown. On Schiermonnikoog, we studied the impact of Greylag foraging on stands of *Spartina anglica*. In a greenhouse experiment, we determined the effects of shoot removal, an aspect of goose grubbing, on the recovery and survival of *Spartina anglica* under both flooded and dry conditions.

*Spartina anglica* was found as a wide belt of vegetation in the lower salt marsh between the third and the fourth creek. Greylags grubbed for rhizomes on both the northern and the southern edges of these stands. They foraged on the below-ground parts of *Spartina anglica* only in areas where it was present in clones, surrounded by bare soil, and that were waterlogged or regularly flooded. The below-ground parts of *Spartina anglica* can probably only be extracted by Greylags in these particular areas. The Greylags preferred grubbing for rhizomes of isolated *Spartina anglica* shoots, which are relatively easy to extract. This enables them to maximise their foraging efficiency. Greylag foraging pressure on *Spartina anglica* was very low. In the most intensively used area, less than 2% was removed.

The greenhouse experiment showed that *Spartina anglica* could survive and recover from shoot removal under dry soil conditions. Under flooded soil conditions, both above- and below-ground survival and recovery of *Spartina anglica* plants was poor, unless the flooding ceased. Shoot recovery in clipped pots was much faster in the dry- than in the flooded treatment. Many new emerging shoots died in flooded-clipped pots, while shoot death was negligible in dry-clipped pots. In only two flooded-clipped pots, shoots could eventually recover after flooding had ceased. In all treatments, the soil was virtually anoxic 1 mm below the soil surface.

Greylags preferably grubbed for *Spartina anglica* rhizomes in flooded areas. Especially in these areas, *Spartina anglica* is most vulnerable. Hence, foraging Greylags could potentially eliminate large parts of the *Spartina anglica* stand on Schiermonnikoog. In our field season, however, goose grazing pressure on *Spartina anglica* was very low. This was mainly caused by the fact that the main food of wintering Greylags was formed by *Scirpus maritimus* tubers. Only when the *Scirpus* marsh will be depleted by grubbing geese, Greylags are expected to intensify their use of the salt marsh as a foraging area. This might eventually result in a significant damage to the *Spartina anglica* stands on Schiermonnikoog.

## 1 INTRODUCTION

Due to the increasing population size of Greylag geese in north-western Europe, wintering Greylags started colonising new staging grounds (Bakker, 1997). The island of Schiermonnikoog, a Dutch Wadden Sea island, is one of these newly colonised areas. Since 1991, approximately 700 Greylags stage and winter on this island.

On the island of Schiermonnikoog, two distinct areas are used by the wintering Greylags. A brackish marsh dominated by *Scirpus maritimus* serves both as a roosting- and a foraging area (Bakker, 1997). The below-ground parts of *Scirpus maritimus* are known to be a traditional food source for wintering Greylags (Amat, 1986; Esselink *et al.*, 1997). The second area used by Greylags is part of the salt marsh, where the geese feed on aerial parts of *Festuca rubra* and *Elymus athericus* and on below-ground parts of *Spartina anglica*. The below-ground parts of a number of *Spartina* species are known to be used by geese (Smith & Odum, 1981; Bélanger & Bédard, 1990; Miller *et al.*, 1996). Only recently however, *Spartina anglica* has been described as a food source for wintering Greylags (Esselink *et al.*, 1997).

*Spartina anglica* is a new graminoid species, that evolved at the end of the 19th century by the hybridisation of the European *Spartina maritima* and the American *Spartina alterniflora* (Gray *et al.*, 1991). Between approximately 1920 and 1940, *Spartina anglica* has been widely planted to stabilise tidal mud flats and currently it occurs in temperate zones throughout the world (Gray *et al.*, 1991). Now, it is one of the dominant species in the pioneer zone of tidal salt marshes (Esselink *et al.*, 1997). In *Spartina anglica*, the production, viability and germination of seeds is highly unpredictable (Hubbard, 1970). *Spartina anglica* largely depends on vegetative reproduction. Young plants expand into circular clones. Such clones may coalesce to form a sward. *Spartina anglica* is usually found as a belt of vegetation immediately seaward of other salt marsh communities. The upper limit of *Spartina anglica* is marked by the successional transition to other salt marsh species. The lower limit is determined by increasing tidal submergence (Gray *et al.*, 1991).

Greylags are one of the first herbivores known to exploit *Spartina anglica* as a food plant. It is found that aerial green parts of most grasses can rapidly regrow after grazing and the same feeding areas may again be used after a few days (Drent & Van der Wal, 1998). Consumption of below-ground parts, however, may lead to the depletion of the resource for the rest of the season or even longer, since rhizomes or tubers show only slow recovery (Amat, 1986; Bélanger & Bédard, 1994). Therefore, goose foraging on below-ground parts of salt marsh plants can be destructive and can result in the complete elimination of vegetation from large areas (Smith & Odum, 1981; Iacobelli & Jefferies, 1991; Esselink *et al.*, 1997). Gray *et al.* (1991) stated that *Spartina anglica* may in the long term be vulnerable to the evolution and spread of herbivores, pests or pathogens. Since Greylags appear to be one of the first herbivores to exploit *Spartina anglica*, it would be interesting to investigate the effects of goose foraging on this new species. In this study, we tried to gain insight in what might happen to the since recently exploited *Spartina anglica* stands on the island of Schiermonnikoog.

It is well known that salt marsh soils are highly reduced and virtually anoxic (Howes *et al.*, 1981; Armstrong *et al.*, 1985). Therefore, the shoots of salt marsh plants are equipped with a well developed aerenchyma to supply their roots with oxygen (DeLaune *et al.*, 1983; Burdick & Mendelssohn, 1990). The leaves, shoots and roots of *Spartina anglica* are highly porous, which enables it to oxidise its root zone (Armstrong *et al.*, 1985). Oxygen in the roots supports aerobic root respiration and eliminates anaerobic phytotoxins like the highly toxic sulphide (H<sub>2</sub>S) (Jordan & Whigham, 1988). The survival of salt marsh plants greatly depends on the capacity to oxidise the root zone and to detoxify the soil phytotoxins, especially in waterlogged soils where oxygen diffuses 10000 times slower than in dry soils (Koch & Mendelssohn, 1989).

In the field we found large numbers of *Spartina anglica* shoots that were pulled out by foraging Greylags. We were interested in what effects this particular aspect of Greylag foraging on *Spartina anglica* would have on the recovery and growth of *Spartina anglica* plants. The removal of shoots would shut down the root oxygen supply and would subject the roots to highly reduced and toxic soil conditions. Thus, shoot removal could have a strong negative effect on the survival of *Spartina anglica* plants. An additive strong negative effect might be expected in flooded soils, where soil conditions are even more reduced. It is especially in such inundated areas that Greylags grub for *Spartina anglica* rhizomes and, consequently, also remove large numbers of shoots. Therefore, *Spartina anglica* might not survive and may totally disappear in grubbed areas.

In an experiment, we investigated whether *Spartina anglica* could survive after shoot removal under both dry and flooded soil conditions.

Our study had two research aims, viz.:

**(1) to establish the significance of *Spartina anglica* as a food plant for Greylag geese,**

and

**(2) to assess the impact of foraging Greylags on *Spartina anglica***

The first aim was covered by Bakker (1997) in a separate report, while this report deals with the second aim. This report consists of two parts. First, I discuss the distribution of *Spartina anglica* on the island of Schiermonnikoog and the impact of Greylag foraging on *Spartina anglica* in the field. Second, I discuss what the effects of artificial shoot removal are on the survival of *Spartina anglica* under both dry and flooded soil conditions.

## **Research questions**

### *Fieldwork*

- Where does *Spartina anglica* occur in relation to the abiotic conditions on the Schiermonnikoog salt marsh?
- Where in the salt marsh do Greylags forage on below-ground parts of *Spartina anglica*?
- Which individual *Spartina anglica* plants are most likely to be attacked by Greylags?
- How much *Spartina anglica* is removed by Greylags on the island of Schiermonnikoog?

### *Greenhouse experiment*

- What are the effects of flooding and clipping on the regrowth and survival of *Spartina anglica*?
- Does flooding affect shoot growth of *Spartina anglica*?
- Is recovery of clipped *Spartina anglica* different under dry and flooded conditions?
- Does the recovery of clipped *Spartina anglica* change when after a period of flooding the dry conditions return?
- Are there differences in soil-oxygen content between the treatments?

## 2 METHODS

### 2.1 Fieldwork

#### 2.1.1 Study site

We studied Greylag foraging on *Spartina anglica* on the island of Schiermonnikoog (53°29'N, 6°12'E), a Dutch Wadden Sea island (Fig. 2.1a). Greylags used two areas on the eastern part of the island (Fig. 2.1b). The first area was the *Scirpus* marsh, a brackish marsh consisting of small dunes surrounded by water. The wettest parts are dominated by *Scirpus maritimus*. On islets and dune edges, *Festuca rubra* is the dominant species. The second area, the salt marsh, covers the south of the east part of the island. It stretches southward from the edges of low dunes to the pioneer zone on the mud flats. The pioneer zone and the lower salt marsh are dominated by a wide belt of *Spartina anglica*. *Salicornia* spp. are also abundant in the pioneer zone. The upper salt marsh consists of different successional stages of vegetation and is dominated (from South to North) by *Atriplex portulacoides*, *Puccinellia maritima*, *Festuca rubra* and *Elymus athericus*.

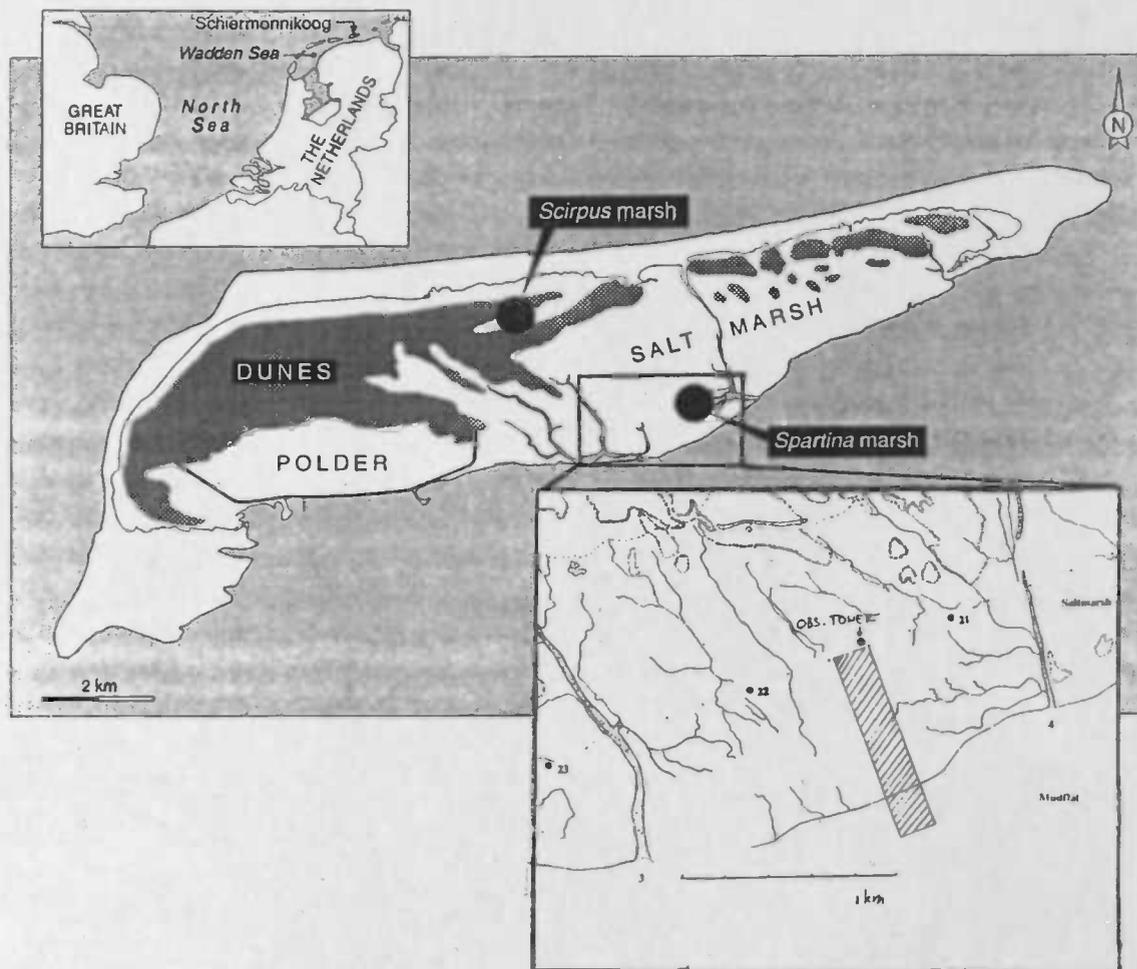


Fig. 2.1. (a) Location of the island of Schiermonnikoog in the Netherlands. (b) The island of Schiermonnikoog with the two different winter areas used by staging Greylag Geese. (c) Location of the study transect, between the third and the fourth creek. Copied from Bakker (1997).

## 2.1.2 Transect

### *Transect description*

In order to gain insight on the relation between Greylag Geese, *Spartina anglica* and abiotic factors, a study transect was established in 1994. This transect (180 m x 850 m), was situated between the third and the fourth creek. It stretched from the inter-tidal mud flats in the south, up to the lower dune edge in the north of the plot area (Fig. 2.1c). In the transect, we measured vegetation cover of all plant species, as well as marsh elevation and clay thickness (Appendix IV, I and II respectively). Furthermore, we built an observation tower in the north-eastern corner of the transect. This enabled us to observe foraging geese. Finally, we conducted a number of experiments in and around the transect.

### *Estimating vegetation cover*

In the transect, we determined total vegetation cover and the cover of all plant species. We surveyed the transect in grid cells of 10 m x 10 m. In each grid cell, we estimated vegetation cover in percentages (Table 2.1). We monitored *Spartina anglica* cover in more detail than other plant species. In each grid cell, we also monitored the presence and absence of gullies. The most southern two thirds of the transect (520 m), were recorded in the autumn of 1994. The upper part of the transect (330 m), was recorded in the autumn of 1995.

Table 2.1. The scales that were applied for the recordings of vegetation cover (first column). *Spartina anglica* cover was recorded with a detailed scale with seven classes (second column). We used a more simple scale, with only four classes, for the other plant species (third column).

score	<i>Spartina</i> cover (%)	cover of other species (%)
.1	< 1	-
.3	1-5	< 5
1	5-15	-
2	15-25	5-25
4	25-50	25-50
6	50-75	-
8	> 75	> 50

### *Marsh elevation*

We measured marsh elevation with a theodolite. In the upper 150 m of the transect, we determined marsh elevation in each 10 m x 10 m grid cell. In the lower parts of the transect, we determined marsh elevation every 20 m. Each time, we skipped one grid cell in the E-W direction and one row of grid cells in the N-S direction. All measuring points were situated in the centre of the grid cells. The obtained field data on marsh elevation are shown in Appendix I.

### *Clay thickness*

We determined clay thickness along one N-S line in the transect. This line ran along the most western border of the transect. Clay thickness was determined by extracting a soil core ( $\varnothing$  2 cm) and measuring the column of clay to the nearest millimetre. Clay could be distinguished from sand on basis of soil texture. We measured clay thickness every 10 m in the upper 150 m of the transect and every 20 m in the rest of the transect. The obtained field data on clay thickness are shown in Appendix II.

#### **2.1.3 Goose grubbing tracks**

Three times, the study transect was monitored on goose grubbing tracks. Monitoring dates were 18 and 27 November and 3 December 1995. During this period, Greylags were still observed foraging in the *Spartina anglica* area. Grubbing tracks were monitored along seven line transects. These line transects ran from the dune edge down to the mud flats. Distance between the transect lines was 30 m. The outermost lines ran along the east and west borders of the transect. Every 25 m, we recorded the presence of *Spartina anglica* stems that were pulled out by geese. At each point, we searched for grubbing tracks in a circular area of approximately 10 m. We distinguished between no grazing (0 shoots), low grazing pressure (1-5 shoots) and high grazing pressure (> 5 shoots).

#### **2.1.4 Removal of individual *Spartina anglica* shoots**

We investigated whether Greylag Geese preferred plants in a specific position when grubbing for *Spartina anglica* rhizomes. A total of 196 *Spartina anglica* shoots were individually marked in an area where foraging Greylags had been observed. These shoots were situated at different positions in a large number of *Spartina anglica* clones. Each shoot was marked with an inconspicuous band of transparent tape. We placed a small numbered PVC tube at a distance of approximately 30 cm from each marked shoot. The PVC tube helped us to relocate the taped *Spartina anglica* shoots. We distinguished between three different shoot positions. Firstly, 56 marked shoots stood in the middle of large *Spartina anglica* clones. Secondly, 68 marked shoots stood in the fringe of *Spartina anglica* clones. Finally, 72 marked shoots were situated outside clones, i.e. at least 10 cm away from a clone's edge. We measured the length of each shoot to the nearest centimetre. Approximately once a week, we recorded the disappearance of the marked shoots. When a marked shoot had disappeared, we searched for it among loose-lying grubbed stems in the near surroundings. The obtained field data on individually marked shoots are shown in Appendix III.

#### **2.1.5 Determining goose foraging pressure**

We established four exclosures of 4 m x 16 m each, with four corresponding controls in areas with high *Spartina anglica* cover. This enabled us to determine goose grubbing pressure. We built two exclosures in the upper marsh, one exclosure in the middle and one exclosure in the most lower regions of the *Spartina anglica* sward. The exclosures were thoroughly wired along all sides and the top was similarly treated. This prevented geese from entering the exclosures. Nevertheless, once or twice a goose was observed within an exclosed area. The control areas were established at a distance of approximately 20 m from each exclosure. *Spartina anglica* cover in each exclosure was approximately the same as in its corresponding control. The boundaries of the controls were marked with inconspicuous sticks in each corner.

All exclosures and controls were monitored in the first two weeks after the plots were established. That was before, or only in the very early stages, of goose visitations. In all control areas, we recorded vegetation cover and *Spartina anglica* stem densities in grid cells of 0.5 m x 0.5 m. In the exclosures, two 2 m x 2 m areas per exclosure were marked with PVC tubes in the corners. As in the controls, these plots were also monitored in 0.5 m x 0.5 m grid cells. We monitored vegetation cover of all species other than *Spartina anglica* according to the '*Spartina*' scale (see table 2.1, second column). Furthermore, we estimated *Spartina anglica* stem densities in the above mentioned areas (table 2.2). In the controls, we mapped the total area that *Spartina anglica* covered. At the end of the season, we monitored one exclosure and corresponding control for a second time. At this period, most geese had left the island. The other three exclosures could not be monitored, since they had been destroyed by drift ice.

Table 2.2. Table that was used to estimate *Spartina anglica* stem densities in 0.5 m x 0.5 m grid cells.

score	estimated number of <i>Spartina anglica</i> shoots / 0.25 m <sup>2</sup>
0	0
1	1-5
2	5-10
3	10-15
4	15-25
5	25-50
6	50-100
7	100-200
8	> 200

## 2.2 Greenhouse experiment

### 2.2.1 Experiment preparation

#### *Collecting, potting and acclimation of experimental plants*

*Spartina anglica* plants were collected on 17 and 29 November 1995 from the salt marsh along the Groningen coast (53°24' N, 6°18' E). The plants were collected with an associated clump of soil, divided into equally sized portions and thus transferred to pots (height = 11 cm; Ø = 15.5 cm). Each pot contained 6-39 tillers of *Spartina anglica*. Other plant species were removed. The pots were placed in a greenhouse with an air temperature of 15°C and a light - dark regime of 14 - 10 hours. The pots were placed in plastic containers (height x width x length = 20 x 30 x 40 cm; 6 pots per container). Subsequently, the plants were left to recuperate for 6 weeks. The water level in the containers was maintained at approximately 5 cm by adding demineralised water if necessary. The plants were sprinkled regularly with demineralised water, to prevent the accumulation of salt excretion on the leaves.

#### *Administration of nutrients and chemicals in the acclimation period*

A nutrient solution (100 ml/pot) was administered twice during the acclimation period. Just before beginning the actual experiment, plants were treated with an insecticide, since almost all plants appeared to suffer from insect infestation. Once the experiment had started, only demineralised water was administered to the plants.

#### *Selection of experimental plants*

After six weeks, 84 pots that contained the highest numbers of living shoots were selected as experimental plants. These were randomly divided over the four treatment groups. The pots were individually labelled and returned in the plastic containers. Each treatment used four containers.

### 2.2.2 Experimental design

#### *Treatment description*

In order to investigate the effects of flooding and of shoot removal on *Spartina anglica* growth, a 2 x 2 factorial experiment was established (Fig. 2.2). This resulted in four different treatments containing 21 pots each. First we used two different water levels. These levels were chosen to simulate dry and flooded marsh conditions. In dry treatments, the water level in the containers was maintained at 5 cm. In the flooded treatments the water level was maintained at 7 cm above the pots' sediment surface. Secondly, we treated the plants in two different ways. These treatments were supposed to simulate an ungrazed (intact) and an extremely grazed (clipped) situation. In the intact treatments, all above ground material was left intact. In the clipped treatments, all above ground material was clipped at soil level.

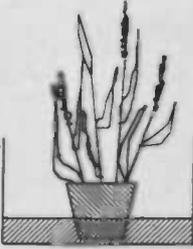
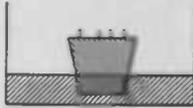
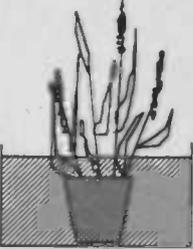
treatment	not clipped	clipped
dry		
wet		

Fig. 2.2. Experimental design for the *Spartina anglica* clipping experiment. The four treatments can be distinguished, i.e. dry-intact, flooded-intact, dry-clipped and flooded-clipped. Water levels in the containers are indicated in grey. N = 21 pots per treatment.

#### *Duration of the experiment*

The pots were subjected to these treatments for five weeks. After these five weeks, we removed eleven pots per treatment to determine above- and below-ground biomass. The remaining pots stayed in the experiment for another 24 days. Water level however, was now maintained at 5 cm in all treatments. Thus, we could determine if clipped plants in the flooded treatment would be able to recover when flooding ceased.

#### **2.2.3 Measurements**

##### *Counting total shoot numbers*

Just before starting the treatments, numbers of living shoots per pot were counted. These data were collected for all four treatments. Similar countings were made after 35 days, at the end of the experiment. See Appendix V.

### *Recovery of clipped plants*

For all pots in the clipped treatments, regrowth of new shoots was monitored by regular countings of emerging shoots (Appendix VI). We counted approximately once a week during the entire experimental period. We distinguished between new shoots, emerging from winter buds, and shoots that emerged from regenerating old shoots. Each new emerging shoot was provided with a small ring of plastic to prevent us from counting newly emerged shoots twice. Only live shoots were counted. We also recorded the numbers of shoots that died. Counting continued until the end of the experiment. This was after 5 weeks for the 22 clipped pots that were harvested for biomass determination and after 8 weeks for the remaining 20 pots.

### *Biomass determinations*

Eleven plants per treatment were harvested after 5 weeks. All above ground parts were clipped at soil level. The soil cores, containing the roots and rhizomes, were removed from their pots and placed on a sieve (mesh size 2 mm). All soil was carefully washed away, leaving only *Spartina anglica* roots and rhizomes behind. Plants were sorted into dead and live material for both above- and below-ground parts. Sorted plant material was placed in paper bags and oven dried for 48 hours at 70 °C. Subsequently, above- and below-ground biomass of live and dead material was determined for each sample (Appendix V).

### *Determination of soil-oxygen content*

After thirty days in the experiment, four pots, one from each treatment, were selected. Two pots containing only soil, one dry and the other flooded, were also taken. These six pots were used to determine soil-oxygen contents.

Oxygen content was measured at several depths in the sediment. We started at the sediment surface and descended the electrode in the sediment in 1 millimetre steps for the first 15 millimetres. In pots containing plants, we also measured oxygen content at depths of 20 and 25 millimetres. In each pot with *Spartina anglica*, this procedure was repeated at 7 different sites. Oxygen content was measured at five different sites in pots containing sediment only.

### 3 RESULTS

#### 3.1 Field work

##### 3.1.1 Abiotic conditions in the transect

On the north edge of the transect, marsh elevation reached a maximum height of 1.49 m above N.A.P. (Fig. 3.1, Appendix I). The minimum elevation in the transect, 0.76 m above N.A.P., was found along the southern edge of the transect. Apart from this distinct N-S gradient in marsh elevation, there was a slight W-E gradient in elevation. The elevation along the western edge of the transect was on average 6 cm higher than along the eastern edge. The average elevation in the N-S direction of the transect showed an overall decline (Fig. 3.2a). From 700 m onwards, marsh elevation dropped more rapidly than in the rest of the transect.

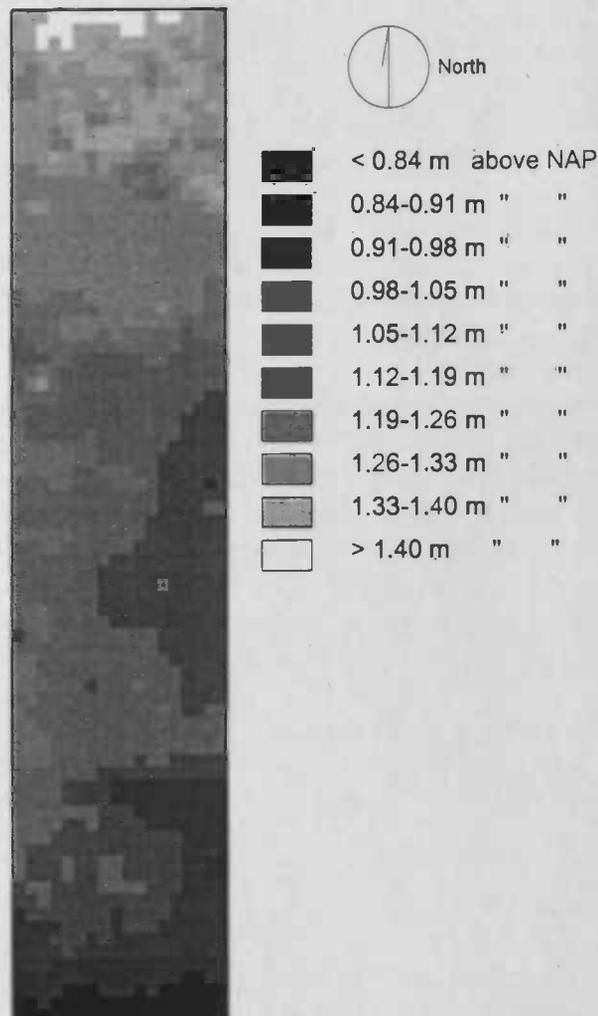


Fig. 3.1. Marsh elevation in the transect. Marsh elevation was divided in 10 classes (see legend). Each grid cell represents an area of 10 m x 10 m in the transect. This map covers the transect from the northern border (top) to 800 m southward (bottom). In the upper 150 m, elevation was measured in each grid cell. More southward, elevation in one of four grid cells was determined (Appendix I). Elevation in other grid cells was interpolated from surrounding data points.

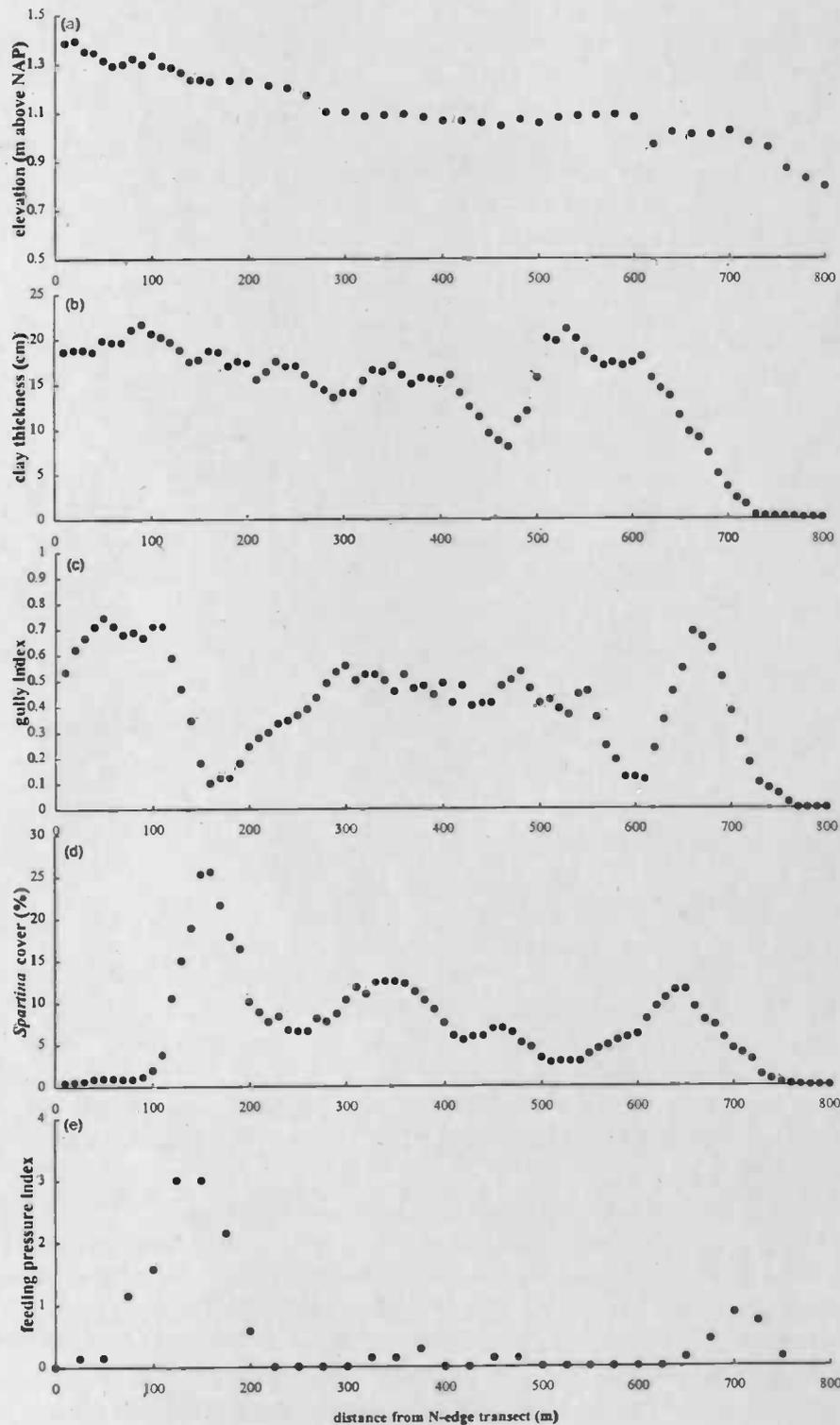


Fig. 3.2. Abiotic conditions, *Spartina anglica* cover and goose foraging pressure in the transect. The northern edge of the transect is at 0 m. The southern edge of the transect is at 800 m. (a) Average marsh elevation (m above N.A.P.) in the N-S direction of the transect. The plotted data points represent the average elevation in each W-E line. N = 18 for the first 15 data points, N = 9 for the other data points. (b) Clay thickness (cm) along the western border of the transect. (c) Gully index. The fraction of grid cells in each W-E line that contained gullies. N = 18 for all data points. An index of 1 indicates that in each grid cell gullies were present. An index of 0 means that no gullies were present. (d) *Spartina anglica* cover (%). Average *Spartina anglica* cover was calculated in each W-E line. Each data point represents the running average between 5 consecutive lines. (e) Goose foraging pressure index. The plotted data points represent the average foraging pressure in each W-E line. N = 7 for all data points.

Clay thickness varied between 22 cm and 13 cm in the northern half of the transect (Fig. 3.2b, Appendix II). There was a slight overall decline in clay thickness in this area. After 400 m, clay thickness suddenly dropped and reached a minimum of 7 cm at 470 m. In the following 50 m, clay thickness increased to over 20 cm. Beyond 600 m, clay thickness dropped almost linearly to 0.2 cm on the inter-tidal flats (750 m). Gullies were abundant in the major part of the transect (Fig. 3.2c). In two areas however, gullies were hardly present. Gullies were sparse between 150 m and 200 m and between 570 m and 620 m from the northern transect edge. There were only few gullies in the most southern 100 m of the transect.

### 3.1.2 Distribution of *Spartina anglica* in the transect

In the most northern part of the transect, *Spartina anglica* cover was very low (Fig. 3.3). In the first 100 m, *Spartina anglica* was absent in more than half of all grid cells. Any *Spartina anglica* that was present in the first 100 m of the transect formed small- to large-sized clones. At 150 m from the northern edge of the transect, *Spartina anglica* cover abruptly changed into a dense stand. This high-density zone continued southward for approximately 70 m. Beyond that, *Spartina anglica* was present in large patches of medium- and low densities. At approximately 700 m from the northern transect edge, the continuous *Spartina anglica* sward ended. *Spartina anglica* occurred for 70 metres further southward, and formed clones similar to those in the most northern 100 m of the transect.

#### *Distribution of other species*

In Appendix IV, maps with the distribution of the other plant species in the transect can be found. Only species that were present in more than 50 grid cells are shown.

#### *Spartina anglica* cover and abiotic conditions

*Spartina anglica* was found mainly in the elevation range between 1.30 m and 0.9 m above N.A.P. (Fig. 3.2a and Fig. 3.2d). *Spartina anglica* was not present at elevations higher than 1.40 m and lower than 0.88 m above N.A.P. (Fig. 3.1 and 3.3). In the N-S direction of the transect, three distinct peaks in *Spartina anglica* cover could be seen (Fig. 3.2d). The first peak, the high density zone, extended from 100 m to 200 m from the north edge of the transect. The second peak was between 300 m and 400 m. Finally, the third peak in *Spartina anglica* cover was between 600 m and 700 m in the transect.

There were differences in abiotic conditions between the three sites where *Spartina anglica* cover peaked (Fig. 3.2). In the high density zone, the average elevation ranged from 1.20 m to 1.28 m above N.A.P. Clay thickness ranged from 17 cm to 20 cm in this area. Overall gully index was low in the high density zone. In the area of the second *Spartina anglica* peak, the average elevation was approximately 1.10 m above N.A.P. In this area, the average clay thickness was 16 cm. Gullies were present in approximately half of all grid cells in this area. In the area of the last *Spartina anglica* peak, elevation ranged from 0.93 m to 1.10 m above N.A.P. In this area, clay thickness decreased linearly from 18 cm at 600 m to 4 cm at 700 m. Gully index was very high in this area.

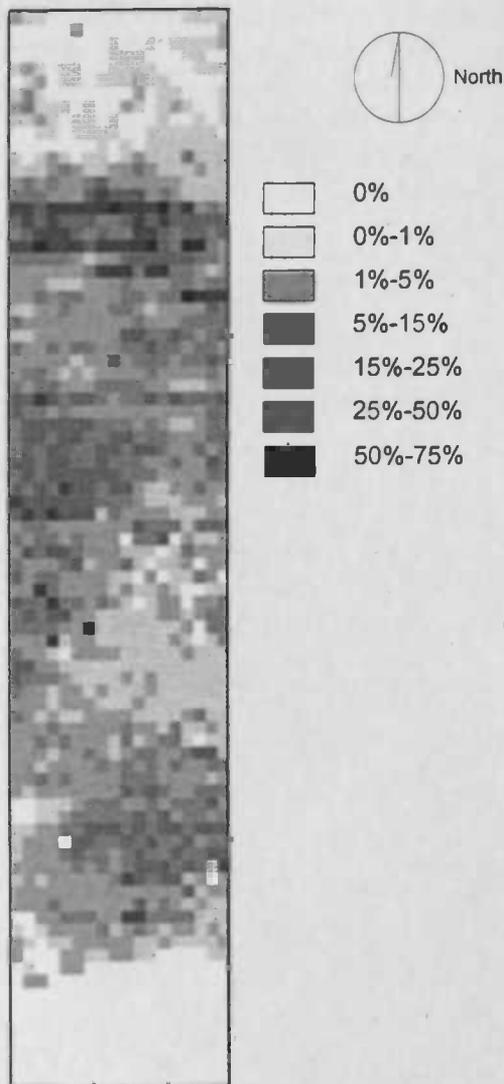


Fig. 3.3. Vegetation map of *Spartina anglica* in the transect. In each grid cell, *Spartina anglica* cover is shown according to the *Spartina* scale (legend). Each grid cell represents an area of 10 m x 10 m in the transect. The top row of grid cells represents the northern edge of the transect. This vegetation map covers the entire transect, down to the southern transect border. The distance between the northern and the southern edges is 850 m.

### 3.1.3 Goose grubbing tracks in the transect

Greylags foraged on both the northern and the southern edges of *Spartina anglica* vegetation (Fig. 3.2d and Fig. 3.2e). In the northern foraging area, Greylag foraging pressure was very high. In the southern foraging area, Greylag foraging pressure was low. The conditions between the two foraging areas were quite different (Fig. 3.2). *Spartina anglica* cover was low in the southern foraging area. In this area, the gully index was intermediate to low. Clay thickness ranged between 0 cm and 10 cm in the southern foraging area. In the first 75 m of the northern foraging area, *Spartina anglica* cover was very low. In the rest of the northern foraging area, *Spartina anglica* cover was intermediate to high. Goose exploitation was highest in this latter area. Gully index was high in the first 75 m of the northern foraging area and intermediate to low in the rest of the northern foraging area. In the northern foraging area, clay thickness was 18 cm on average.

Fig. 3.4 shows the transect area that was used by Greylags in more detail compared to Fig. 3.2e. Greylag grubbing tracks were mainly found in the northern part of the transect, especially in and along the northern edge of the high density zone. Occasionally, low goose exploitation was observed in the middle of the transect. The south western corner of the *Spartina anglica* sward was also used as a goose foraging area. Goose grubbing tracks were mostly found at transitions between low and high *Spartina anglica* cover or at the edges of *Spartina anglica* clones.

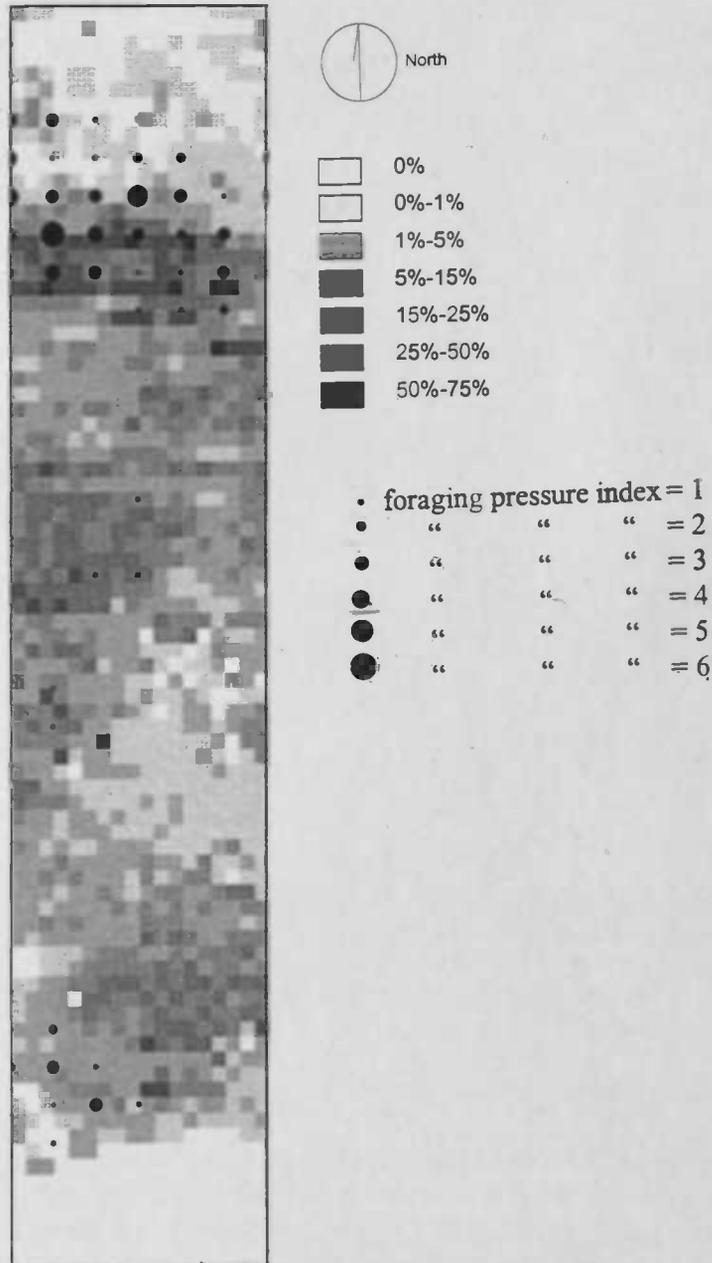


Fig. 3.4. Goose foraging areas in the transect. *Spartina anglica* cover is shown as in Fig. 3.3. Greylag foraging activity is indicated by white spots. Small spots represent low foraging pressure, larger spots represent higher foraging pressures.

### 3.1.4 Goose preference for plant position

A total of 16 individually marked *Spartina anglica* tillers were removed by Greylags (Table 3.1). All of these were free standing shoots. Thus, more than 20% of the marked free standing shoots disappeared. Shoots were not removed from the fringes or the centres of clones. Almost all marked shoots that had been removed were found amongst grubbed debris in the vicinity of their original position.

Table 3.1. Removal of individually marked *Spartina anglica* shoots.

Shoot position	# marked shoots	# shoots removed
centre of clone	56	0
fringe of clone	68	0
isolated shoot	72	16

### 3.1.5 Goose foraging pressure

In the enclosure, no *Spartina anglica* had disappeared from the 2 m x 2 m grids (personal observation). In the control area, some *Spartina anglica* had disappeared due to exploitation by Greylags (Fig. 3.5, Table 3.2). However, goose foraging pressure in the control area was very low. Less than 2% of the entire *Spartina anglica* stand was removed during the 1995/96 season. The Greylags foraged mainly on the smallest *Spartina anglica* clones and on the edges of a few large clones. Almost all free standing shoots had disappeared. Most large clones were not affected.

Table 3.2. Numerical data concerning the control area. Surface area and percentages of the areas with and without *Spartina anglica* are shown. Data in the bottom line represent the total surface area of *Spartina anglica* that was removed and the percentage of total *Spartina anglica* cover that was removed respectively.

	surface area (m <sup>2</sup> )	%
entire control area (4 m x 16 m)	64.00	100.0
area without <i>Spartina anglica</i>	37.84	59.0
area covered by <i>Spartina anglica</i>	26.16	41.0
area of <i>Spartina anglica</i> removed	0.46	1.8

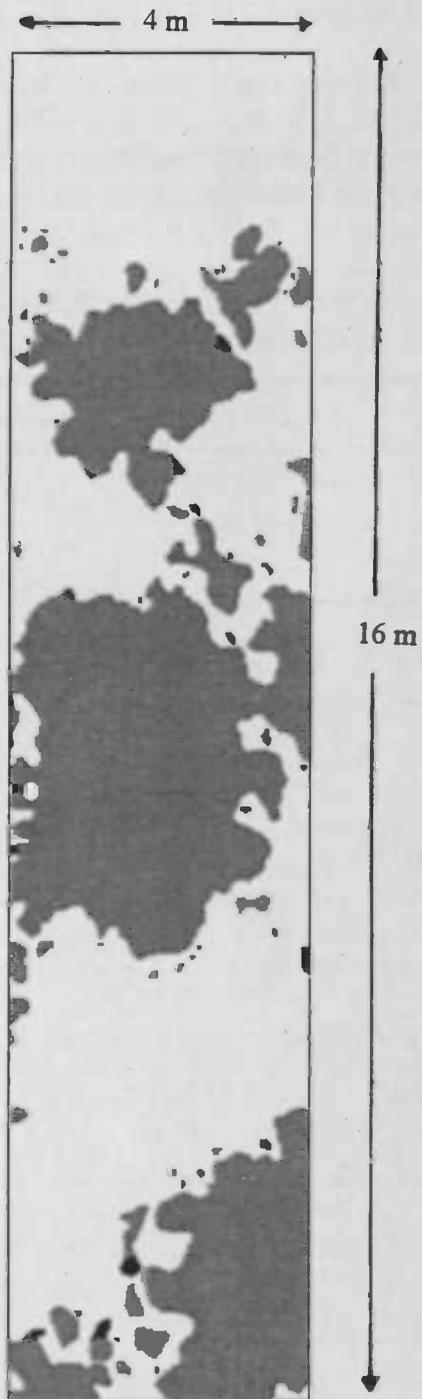


Fig. 3.5. Map of *Spartina anglica* cover in the control area. The area that was covered by *Spartina anglica* at the end of the season is show in light grey. Dark grey patches represent the area of *Spartina anglica* that was removed by geese. *Spartina anglica* was never found in the white areas.

## 3.2 Greenhouse experiment

### 3.2.1 Total numbers of shoots before and after treatments

Before the treatments were initiated, the average number of shoots per pot did not differ significantly between groups (oneway anova,  $F_{3,80} = 0.21$ , n.s.; Fig. 3.6a). At the end of the experiment, there was a highly significant treatment effect (oneway anova,  $F_{3,80} = 34.7$ ,  $P < 0.001$ ; Fig. 3.6b). After 35 days, there was no difference between dry-unclipped and flooded-unclipped pots. The final number of shoots in both clipped treatments was lower than in both unclipped treatments. Moreover, the final number of shoots in flooded-clipped pots was lower than in the dry-clipped pots. After five weeks, the final number of shoots in both dry-unclipped and flooded-unclipped pots did not differ significantly from initial shoot numbers (oneway anova,  $F_{1,40} = 3.0$ ,  $P = 0.1$  and  $F_{1,40} = 1.1$ , n.s. respectively). At the end of the experiment, shoot numbers in both dry-clipped and flooded-clipped pots were significantly lower than five weeks earlier (oneway anova,  $F_{1,40} = 5.1$ ,  $P < 0.05$  and  $F_{1,40} = 34.3$ ,  $P < 0.001$  respectively).

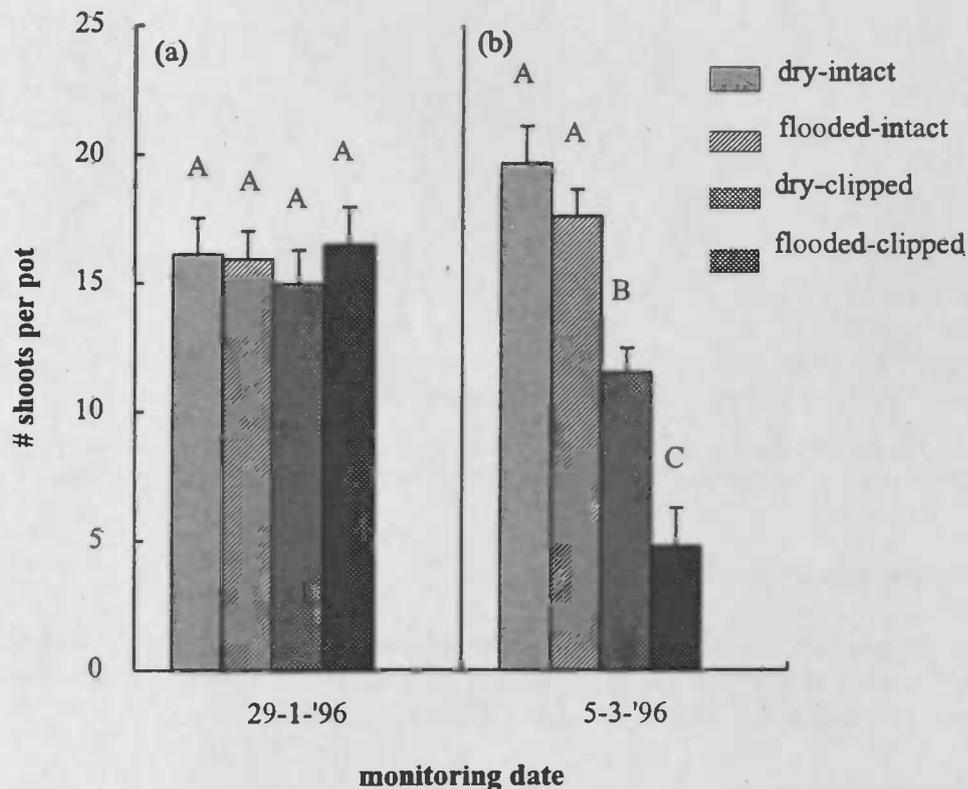


Fig. 3.6. Average number of shoots per pot, before and at the end of the experiment for each treatment group (see also Appendix V). (a) Average number of shoots per pot before treatment initiation. (b) Average number of shoots per pot after 35 days in the experiment.

### 3.2.2 Above- and below-ground biomass after treatments

#### *Live above-ground biomass*

After 35 days, there was a significant treatment effect on live above-ground biomass (oneway anova,  $F_{3,40} = 40.9$ ,  $P < 0.001$ ; Fig. 3.7). There was no significant difference between dry-unclipped and flooded-unclipped plants. Above-ground biomass differed significantly between clipped and unclipped plants. There was no significant difference between dry-clipped and flooded-clipped plants. When tested separately however, the difference between dry-clipped and flooded-clipped plants was significant (oneway anova,  $F_{1,20} = 4.7$ ,  $P < 0.05$ ).

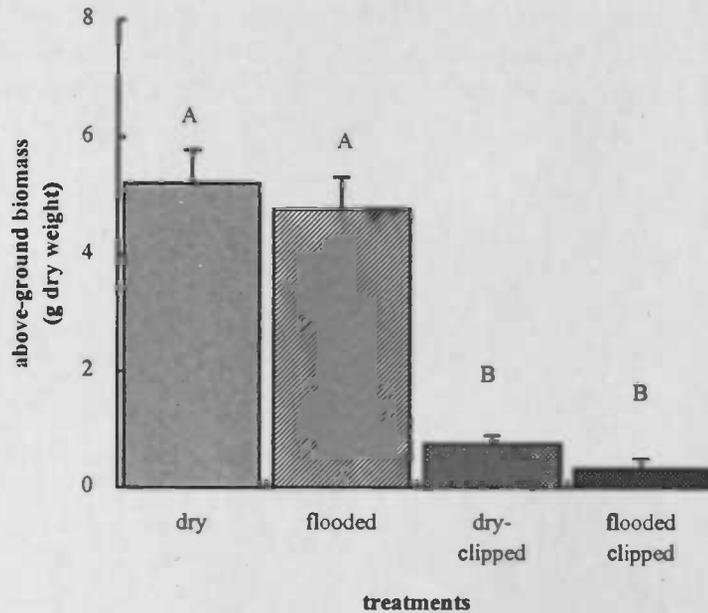


Fig. 3.7. Live above-ground biomass (mean  $\pm$  SE) after 35 days for each treatment (see Appendix V). Biomass of live plant material is given as gram dry weight per pot. Eleven pots per treatment were measured.

#### *Dead above-ground biomass*

Dry-unclipped pots, contained significantly more dead above ground biomass than pots in the flooded-unclipped treatment (oneway anova,  $F_{1,18} = 6.9$ ,  $P < 0.05$ ; Fig. 3.8). Dead above-ground material was hardly present in both clipped treatments.

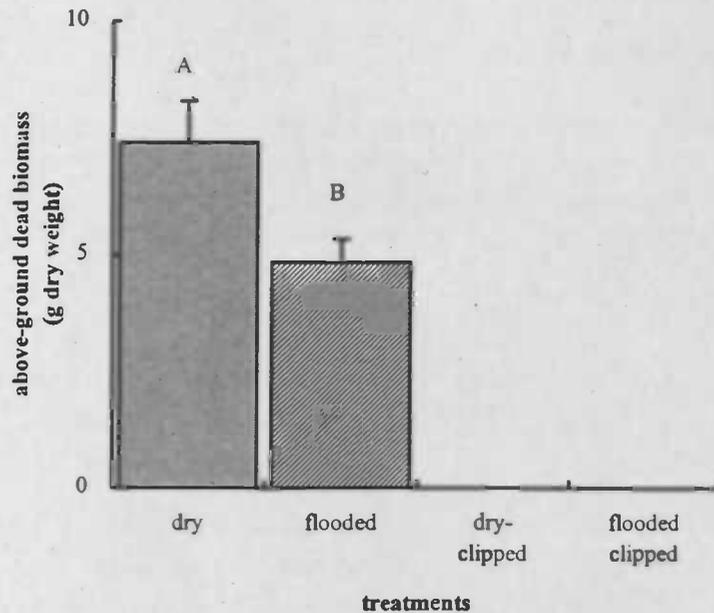


Fig. 3.8. Dead above-ground biomass per pot (mean dry weight  $\pm$  SE) at the end of the experiment. N = 11 for flooded-unclipped pots, N = 9 for dry-unclipped pots. In the clipped treatments, there was no harvestable dead above-ground material, because the dead particles were too small and most of it had decayed. We therefore considered dead above-ground weight to be negligible.

#### *Live below-ground biomass*

At the end of the experiment, a significant treatment effect on live below ground biomass was found (oneway anova,  $F_{3,40} = 14.4$ ,  $P < 0.001$ ; Fig. 3.9). Both flooding and clipping had a negative effect on live below-ground dry weight. Below-ground biomass was highest in dry-unclipped pots. Below-ground biomass was intermediate in both flooded-unclipped and dry-clipped pots. The flooded-clipped pots had by far the lowest below-ground biomass.

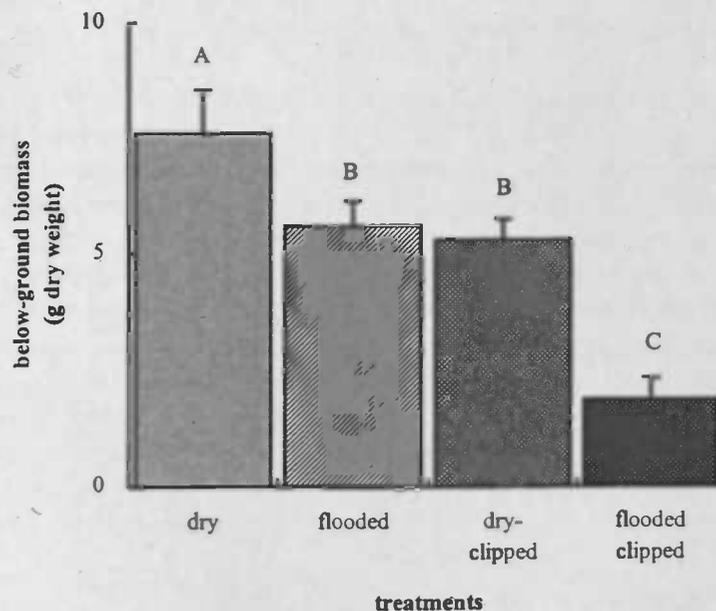


Fig. 3.9. Live below-ground biomass in g dry weight per pot (mean  $\pm$  SE) after 35 days in the experiment (see Appendix V). N = 11 per treatment.

### Dead below-ground biomass

After 35 days, there was a significant treatment effect on dead below-ground biomass (oneway anova,  $F_{3,40} = 3.7$ ,  $P < 0.05$ ; Fig. 3.10). Dead below-ground biomass seemed to be higher in both flooded treatments compared to both dry treatments. This difference however, was only significant between the dry-clipped treatment and the flooded-unclipped treatment.

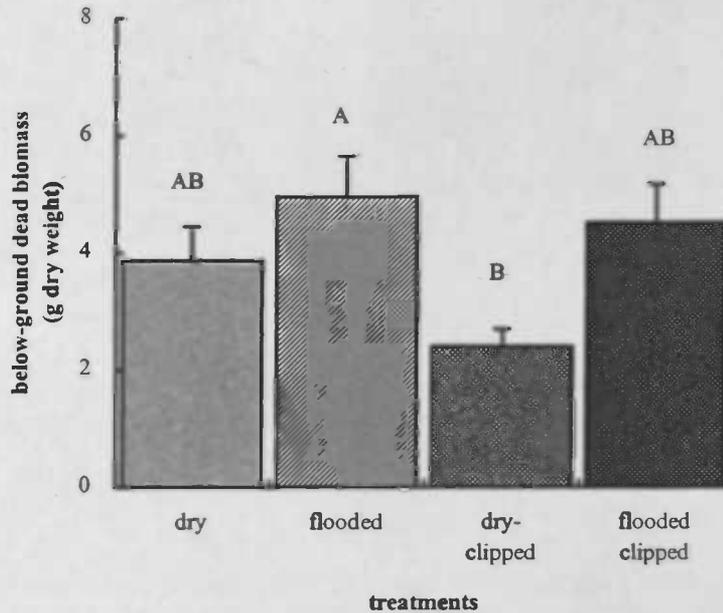


Fig. 3.10. Dead below-ground biomass per pot (mean  $\pm$  SE) after 35 days in the experiment. Data are presented as average weight of below-ground dead material in gram of dry weight per pot.  $N = 11$  per treatment.

### Percentage of live material below ground

After five weeks, there was a significant treatment effect on the percentage of live material below ground (oneway anova,  $F_{3,40} = 12.2$ ,  $P < 0.001$ ; Fig. 3.11). The percentage of live material below ground did not differ between both dry treatments and the flooded-unclipped treatment. However, the percentage of below-ground live material was significantly lower in flooded-clipped pots compared to the other three treatments.

Figure 3.12 shows the percentage of live below-ground material for each pot. Thus, the condition in each pot can be determined. The ten pots with the highest percentage of live below-ground parts, were all from the two dry treatment groups. Of the ten lowest scoring pots, only one was from a dry treatment group. However, data in all treatment groups were approximately in the same range, except for flooded-clipped pots. Only four pots in the flooded-clipped treatment had more than 25% live material below ground. In contrast, none of the other treatments had pots with less than 25% live material below ground.

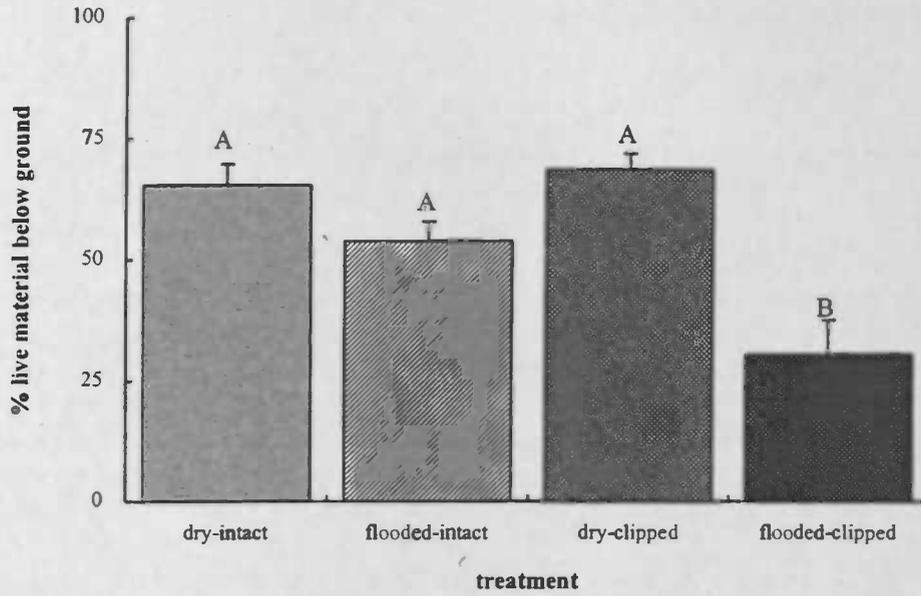


Fig. 3.11. Percentage of below-ground live material per pot (mean  $\pm$  SE), after 35 days in the experiment (see Appendix V). These data were calculated with the following formula:  $100 * ((\text{below-ground live biomass}) / (\text{below-ground live biomass} + \text{below-ground dead biomass}))$ .  $N = 11$  for all treatments.

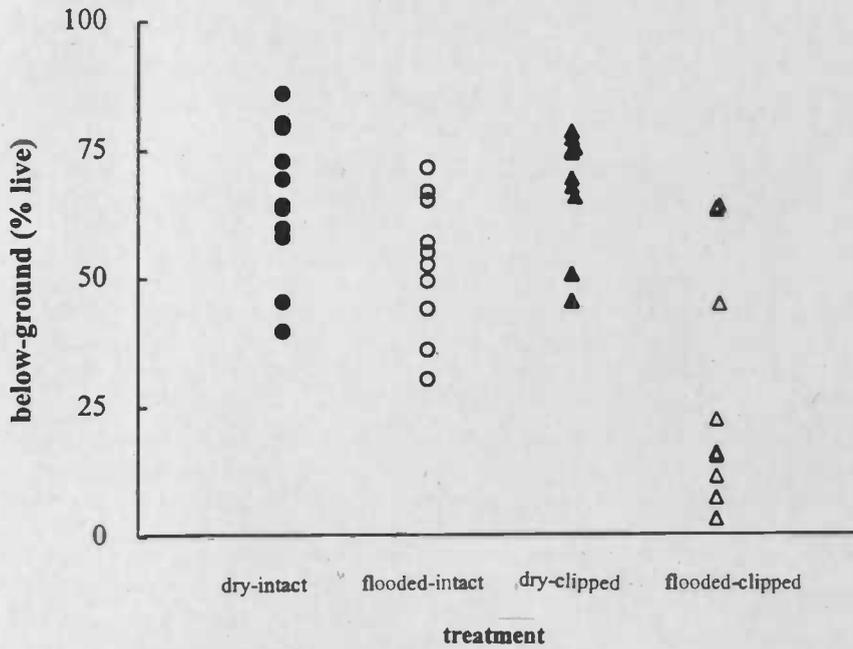


Fig. 3.12. Percentage of live material below ground in each experimental pot (see Appendix V). Each point represents the percentage of one single pot. Each of the four groups (lines) of points represents another treatment.  $N = 11$  in all treatments.

### 3.2.3 Regrowth of shoots in clipped pots

#### *Emerging new shoots*

New shoots emerged two days after clipping under both dry and flooded conditions. Fig. 3.13 shows the total number of new shoots that were alive on each monitoring date. After two days, the average number of new emerging shoots already differed significantly between the two clipping treatments (Mann-Whitney test,  $U = 134.5$ ,  $P < 0.05$ ). In the dry treatment, the average number of new shoots increased steadily in time. In the flooded treatment, the average number of new shoots increased only in the first week. Following this first week, very few new shoots emerged in the flooded treatment and many shoots that had already emerged died. Therefore, the average number of new shoots in flooded pots declined during the rest of the experiment. In the dry treatment, only 6 out of 98 newly emerged shoots died. This was in sharp contrast to the flooded treatment, where a total of 24 out of 39 new shoots died. At the end of the experiment, shoot numbers differed significantly between both treatments (Mann-Whitney test,  $U = 25.5$ ,  $P < 0.001$ ).

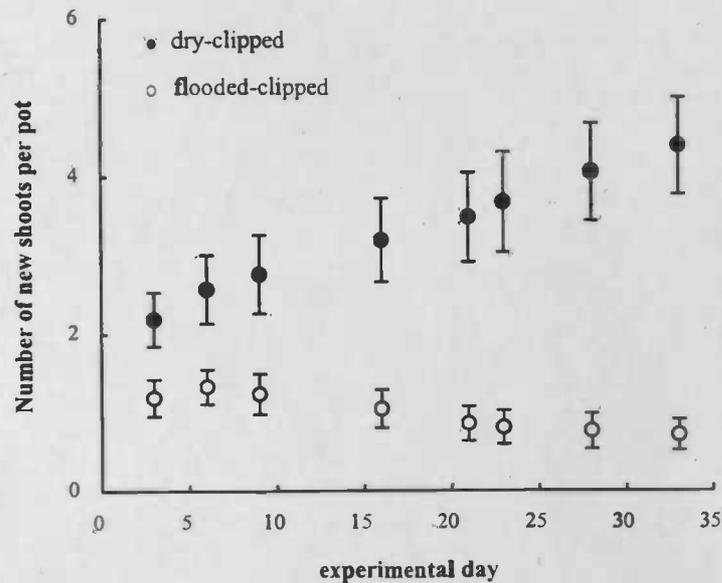


Fig. 3.13. The number of new live shoots (mean  $\pm$  SE) at each monitoring date for the clipped treatments (see Appendix VI). Data is presented in average number of shoots per pot.  $N = 21$  pots per treatment.

#### *Regrowth from clipped shoots*

The first regrowth from the cores of clipped shoots occurred after two days in the dry treatment and after five days in the flooded treatment. In both dry and flooded pots, the average number of regrowing shoots increased rapidly during the first ten days (Fig. 3.14). Later, regrowth slowed down considerably. In the dry treatment, the average number of live regrowing shoots increased until the end of the experiment. In flooded pots, the average number of live regrowing shoots declined after 22 days. In the dry treatment, none of the regrowing shoots died. In the flooded treatment, however, 20 out of 104 regrowing shoots died. The difference in regrowing shoot numbers between dry and flooded pots first became significant after 15 days (Mann-Whitney test,  $U = 138$ ,  $P < 0.05$ ). This difference remained significant until the last monitoring date (Mann-Whitney test,  $U = 111.5$ ,  $P < 0.01$ ).

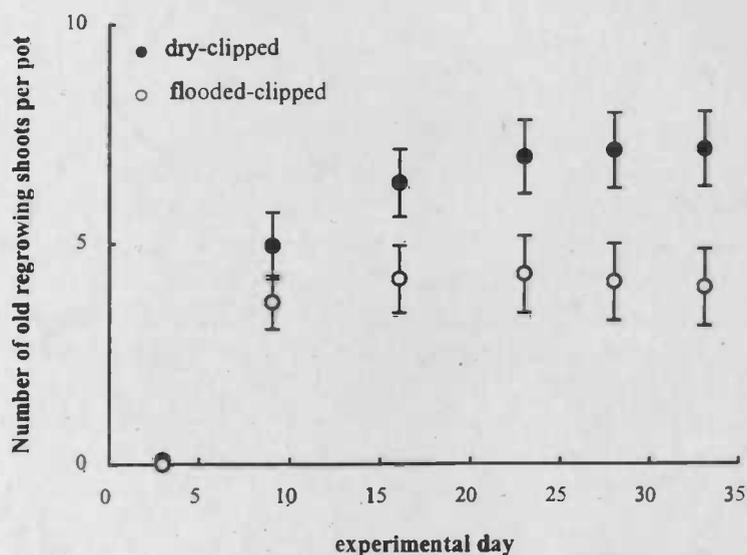


Fig. 3.14. The number of regrowing old shoots (mean  $\pm$  SE) at each monitoring date for the clipped treatments (see Appendix VI). Data is presented in average number of shoots per pot. N = 21 pots per treatment.

Regrowth from clipped shoots is dependent on the number of shoots that were present just before clipping. In the dry treatment, on average almost half of all clipped shoots showed regrowth compared to approximately one third in the flooded treatment (Table 3.3). In the end however, an average of only 21% of all clipped shoots survived in the flooded treatment (Table 3.3).

Table 3.3. Regrowth of clipped shoots under dry and flooded conditions. The first column gives the average number of regrowing shoots per pot. The average number of shoots prior to clipping is shown in the second column. The third column gives the survival ratio (number of regrowing shoots divided by the number of shoots prior to clipping). Several regrowing shoots died under flooded conditions. Therefore, two different ratios were calculated for the flooded treatment. The first value is a potential survival ratio. This represents the ability of clipped shoots to regrow under flooded conditions. The second value is the actual survival ratio. This represents the ability of clipped shoots to survive a 32 day period of flooding. N = 21 pots per treatment.

treatment	# of shoots		regrowth ratio
	before clipping	regrowing	
dry-clipped	15.0 $\pm$ 5.0	7.1 $\pm$ 3.9	0.47 $\pm$ 0.18
flooded-clipped			
- shoots with regrowth	16.5 $\pm$ 7.9	5.0 $\pm$ 4.0	0.28 $\pm$ 0.16
- shoots that survived	16.5 $\pm$ 7.9	4.0 $\pm$ 4.0	0.21 $\pm$ 0.17

### 3.2.4 Recovery of clipped shoots after long-term flooding

#### *Recovery of new emerging shoots*

After 32 days, we lowered the water level in the flooded treatment to the same level as that in the dry treatment. In the dry treatment, the increase in the average number of new emerging shoots remained more or less constant (Fig. 3.15). When flooding ceased, the average number of new emerging shoots increased rapidly in the flooded treatment. In the flooded treatment, no new emerging shoots died after the water level was decreased. At the end of the experiment the average number of new emerging shoots in the flooded treatment was 2.2 shoots per pot. This was more than three times higher than the average shoot numbers at the last day of flooding (0.6 shoots per pot). At the end of the experiment, the difference between dry pots and previously flooded pots was still significant (Mann-Whitney test,  $U = 20.5$ ,  $P < 0.05$ ). However, this was less significant than on the final day of flooding (Mann-Whitney test,  $U = 8$ ,  $P < 0.005$ ).

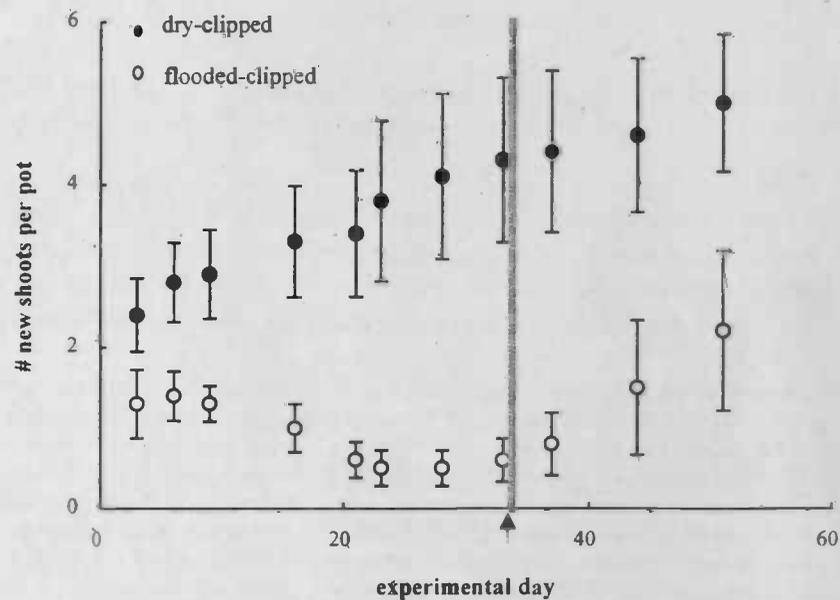


Fig. 3.15. The number of new live shoots (mean  $\pm$  SE) at each monitoring date for the clipped treatments (see Appendix VI). Data is presented in average number of shoots per pot.  $N = 10$  pots per treatment. After 32 days, flooding was ceased in the flooded treatment. This date is indicated by the grey bar and the arrow pointing towards the x-axis.

### Recovery of regrowing clipped shoots

In both the dry and the flooded treatment, the average number of regrowing clipped shoots increased in the first 22 days (Fig. 3.16). After 27 days, the average number of regrowing shoots remained constant in the dry treatment. In the flooded treatment, the average number of regrowing shoots slightly declined after 22 days. When flooding ceased, a slight increase in regrowing shoots was observed in the flooded treatment. After that, the average number of regrowing shoots remained constant. After flooding had ceased, no regrowing clipped shoots died in the previously flooded treatment. During the entire experiment, the average number of regrowing shoots was higher in the dry treatment. However, with  $n = 10$ , this was not significant at any monitoring date.

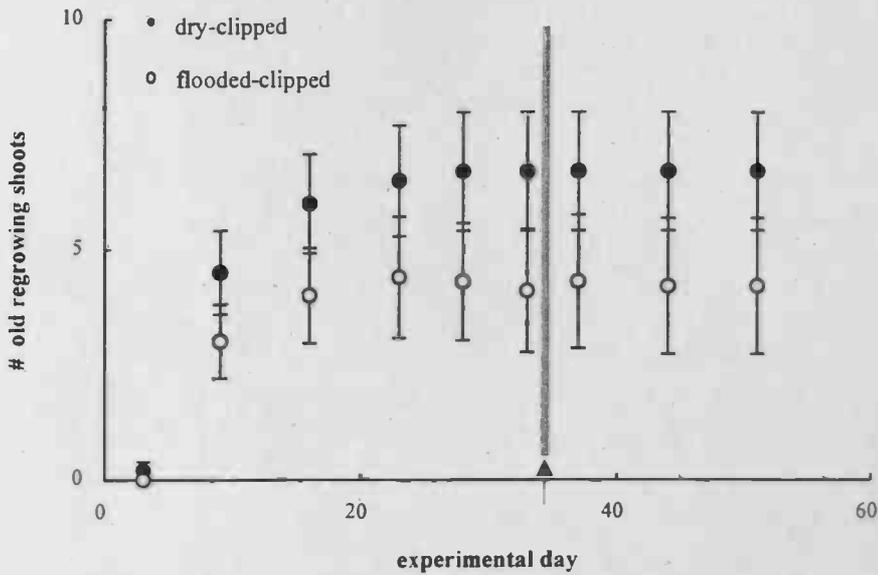


Fig. 3.16. The number of regrowing clipped shoots (mean  $\pm$  SE) at each monitoring date (see Appendix VI). Data is presented in average number of shoots per pot.  $N = 10$  pots per treatment. After 32 days, flooding was ceased in the flooded treatment. This is indicated by the grey bar and the arrow at the x-axis.

### 3.2.5 Soil-oxygen content

Soil-oxygen content was low in all treatments, as well as in the blank soil pots. In all pots, soil oxygen content decreased rapidly with depth (Fig. 3.17, Table 3.4). On the soil surface and in the very first millimetres below the soil surface oxygen content was relatively high. Below 5 mm, the soil was practically anoxic. That is, oxygen content had decreased to approximately 10-15% of saturated water in all pots. Soil-oxygen content in the dry treatments was slightly higher on the surface compared to the flooded treatments (Table 3.4).

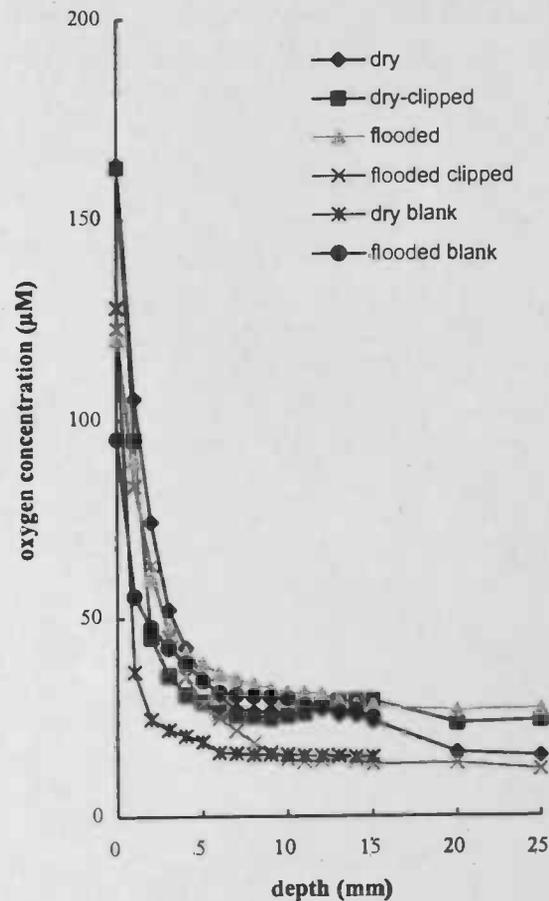


Fig. 3.17. Soil oxygen content at different depths in six different experimental pots. Oxygen content is presented in  $\mu\text{M}$  ( $M = \text{mol/l}$ ). Water saturated with oxygen has an  $\text{O}_2$  concentration of  $235 \mu\text{M}$ . These values were measured in one pot per treatment. Two blank pots, containing only soil, were also measured. One of these blank pots was left dry and the other was flooded. Each experimental pot was probed at seven sites, the blank pots at five different sites. Probing depths were, every millimetre from the surface down to a depth of 15 mm, then 20 mm and finally 25 mm below the surface. These last depths were not probed in the blank pots.

Table 3.4. Soil oxygen content at different depths in six different experimental pots. Oxygen content is presented in  $\mu\text{M}$  ( $\pm$  standard deviation). Oxygen content of saturated water is  $235 \mu\text{M}$ . The values were measured in one pot per treatment.  $N = 7$  probes in the experimental pots and  $N = 5$  probes in the soil pots. The soil pots were not probed at 20 and 25 mm.

depth (mm)	treatments					
	dry			clipped		
	intact	clipped	blank	intact	clipped	blank
0	164 $\pm$ 33	163 $\pm$ 43	128 $\pm$ 38	120 $\pm$ 38	123 $\pm$ 47	95 $\pm$ 34
1	105 $\pm$ 34	95 $\pm$ 44	37 $\pm$ 14	90 $\pm$ 32	83 $\pm$ 52	55 $\pm$ 22
2	74 $\pm$ 34	45 $\pm$ 21	25 $\pm$ 14	60 $\pm$ 23	63 $\pm$ 49	48 $\pm$ 18
3	52 $\pm$ 30	36 $\pm$ 12	22 $\pm$ 12	47 $\pm$ 18	45 $\pm$ 41	43 $\pm$ 16
4	42 $\pm$ 30	31 $\pm$ 7	20 $\pm$ 9	41 $\pm$ 15	35 $\pm$ 32	39 $\pm$ 14
5	35 $\pm$ 23	29 $\pm$ 6	19 $\pm$ 6	39 $\pm$ 13	28 $\pm$ 26	34 $\pm$ 11
6	30 $\pm$ 19	26 $\pm$ 5	16 $\pm$ 4	36 $\pm$ 12	25 $\pm$ 22	31 $\pm$ 8
7	27 $\pm$ 15	26 $\pm$ 4	16 $\pm$ 3	35 $\pm$ 11	22 $\pm$ 19	31 $\pm$ 8
8	26 $\pm$ 13	25 $\pm$ 4	16 $\pm$ 3	33 $\pm$ 10	19 $\pm$ 15	30 $\pm$ 8
9	26 $\pm$ 15	25 $\pm$ 3	16 $\pm$ 3	32 $\pm$ 9	16 $\pm$ 13	30 $\pm$ 7
10	26 $\pm$ 15	25 $\pm$ 4	16 $\pm$ 3	31 $\pm$ 9	14 $\pm$ 11	30 $\pm$ 7
11	26 $\pm$ 17	26 $\pm$ 5	15 $\pm$ 2	31 $\pm$ 9	14 $\pm$ 10	28 $\pm$ 5
12	27 $\pm$ 20	28 $\pm$ 11	15 $\pm$ 2	31 $\pm$ 11	14 $\pm$ 11	28 $\pm$ 5
13	26 $\pm$ 21	29 $\pm$ 13	15 $\pm$ 2	29 $\pm$ 7	15 $\pm$ 13	26 $\pm$ 4
14	25 $\pm$ 22	29 $\pm$ 13	15 $\pm$ 1	28 $\pm$ 6	14 $\pm$ 12	27 $\pm$ 5
15	24 $\pm$ 19	29 $\pm$ 14	15 $\pm$ 1	28 $\pm$ 7	13 $\pm$ 10	25 $\pm$ 3
20	16 $\pm$ 5	23 $\pm$ 2	-	27 $\pm$ 6	13 $\pm$ 12	-
25	15 $\pm$ 4	24 $\pm$ 4	-	27 $\pm$ 6	12 $\pm$ 9	-

## 4 DISCUSSION

### 4.1 Field work

#### 4.1.1 Relations between abiotic conditions, *Spartina anglica* and goose foraging

##### *Occurrence of Spartina anglica in relation to abiotic conditions*

On the island of Schiermonnikoog, *Spartina anglica* occurred as a wide belt of vegetation in the lower salt marsh between the third and the fourth creek (Figure 3.2 and Figure 3.3). In the most northern 100 meters in the transect, *Spartina anglica* hardly occurred. This might be due to the successional replacement of *Spartina anglica* by other salt marsh species (Gray *et al.*, 1991). *Spartina anglica* was probably out-competed by other salt marsh species that grow better in these more elevated areas. In the most southern 100 meters in the transect, *Spartina anglica* also hardly occurred. Gray *et al.* (1991) state that the lower limit of *Spartina anglica* is determined by the increasing tidal submergence. The elevation in the south 100 m of the transect was approximately 10-30 cm below mean high tide, which is 1 m above N.A.P. (Figure 3.1 and Figure 3.2). Consequently, young *Spartina anglica* plants, growing in that area, would be totally submerged at high tides. This might prohibit establishment and growth of *Spartina anglica* in the southern part of the transect.

The occurrence of *Spartina anglica* did not appear to be directly related to clay thickness and the presence or absence of gullies (Figure 3.2). However, the fast declining clay thickness in the southern edge of the transect might also be of slight influence to the decline of *Spartina anglica* in that area. *Spartina anglica* is known to grow in a wide variety of substrates (Gray *et al.*, 1991). Nevertheless, it will grow better in clay than in bare sand, since the clay will contain more nutrients and *Spartina anglica* needs high amounts of nitrogen for its growth (van Schreven, 1958). The highest density of *Spartina anglica* occurred between 100 and 200 meters from the north edge of the transect. In October and November of 1995, this area was permanently inundated and had a water level of approximately 5-10 cm above soil level. The permanent waterlogging in this area might have caused *Spartina anglica* to be present in such high densities, since *Spartina anglica* is the only salt marsh species (apart from *Salicornia* spp.) that can grow and even thrive under such reduced conditions.

##### *Greylag foraging sites*

There were two sites in the transect where Greylags grubbed for the below-ground parts of *Spartina anglica* (Figure 3.2 and Figure 3.4). Both of these foraging sites were situated at the edges of the *Spartina anglica* stand. In these two areas, *Spartina anglica* occurred in large and small clones, mainly surrounded by bare soil. Some other salt marsh species were also present in this area, but only at very low densities. In the middle of the transect, *Spartina anglica* occurred as a more or less continuous sward.

In the transect, the Greylags foraged on *Spartina* rhizomes till the end of November. From then on, the ground had frozen hard and no rhizomes could be extracted. The northern foraging area was permanently inundated while the Greylags were foraging there in October and November of 1995. The southern foraging area was not permanently inundated, but the elevation in this area was below mean high tide (M.H.T.). Therefore, this area was inundated during high tides. There were probably two reasons why Greylags only foraged in these two areas. First, the occurrence of *Spartina anglica* in separate clones might have facilitated the extraction of *Spartina anglica* rhizomes. It will be easier to extract a rhizome while working from the vegetation's edge since, in the middle of a clone or in a sward, *Spartina* rhizomes are much more interconnected.

Second, both areas were either permanently or regularly inundated in the period when the geese foraged on *Spartina anglica*, i.e. October-November (personal observation). Goose grubbing might only be effective in such flooded areas, since only in water the below-ground parts can be easily loosened from the soft soil by repetitive trampling. Probably it is only possible for Greylags to uproot *Spartina anglica* rhizomes in these areas. Maybe the below-ground parts of *Spartina anglica* in the rest of the transect were inaccessible to Greylags. Consequently, it is likely that only a small part of the *Spartina anglica* stand on the island of Schiermonnikoog can be exploited by Greylag Geese.

#### 4.1.2 Goose preference for plant position

Foraging Greylags highly preferred solitary shoots above shoots in the fringes or the centre of a clone (Table 3.1). This is probably due to the fact that rhizomes of free standing shoots can be extracted with much less effort than those of shoots in clumps. Rhizomes of free standing shoots are only surrounded by clay and can be easily uprooted. In contrast, the below-ground parts of shoots in clumps are entangled in the rhizomes of other shoots. A goose will have to work hard to pull these rhizomes loose. In other studies it was found that goose density within *Scirpus* marshes was positively related to the softness of the substrate (Bélanger & Bédard, 1994b; Bélanger & Bédard, 1995). Amat (1986) found that Greylags preferred foraging on small below-ground parts of *Scirpus maritimus*, since this markedly decreased the handling time of food items. All this indicates that geese preferably extract the most easily attainable food items. In doing so, goose handling time will decrease and relatively more energy can be obtained in less time. Possibly, the Greylags on the island of Schiermonnikoog tried to maximise their cost/benefit ratio by grubbing for free standing *Spartina anglica* shoots and, as mentioned in section 4.1.1, by foraging in areas with soft inundated substrates.

#### 4.1.3 Goose foraging pressure

In the winter of 1995, goose utilisation of *Spartina anglica* was very low. In one control area, less than 2% of the *Spartina anglica* cover was removed (Figure 3.5 and Table 3.2). The control area was situated in the transect part where most Greylag grubbing tracks had been found. Therefore, goose foraging pressure in the entire transect will even have been lower than in the control area. From this it can be concluded that, only a minor part of the total stand of *Spartina anglica* in the transect was removed by geese. This was in part due to the fact that the Greylags did not only roost in the *Scirpus* marsh, but also foraged there on *Scirpus maritimus* tubers, part of the time. Hence, at the moment the traditional Greylag food, *Scirpus maritimus*, appears to be the most important food species for wintering Greylags on the island of Schiermonnikoog. Since the total area of *Scirpus maritimus* on the island of Schiermonnikoog is not very large, increased goose visitation could lead to the depletion of *Scirpus* as a food stock. In that case, Greylags might show an increased use of the salt marsh as a foraging area. Consequently, the impact of Greylag foraging on *Spartina anglica* could increase.

Due to strong frost, Greylags could only forage on *Spartina anglica* until the end of November. After that, *Spartina anglica* rhizomes became inaccessible for the geese. Thus, the period in which the Greylags could forage on *Spartina anglica* was very short. This might be another important reason for the extremely low foraging pressure on the *Spartina anglica* stand on the island of Schiermonnikoog. Goose foraging pressure on *Spartina anglica* might be much higher in mild winters.

## 4.2 Greenhouse experiment

### 4.2.1 Total number of shoots before and after treatments

In five weeks, the number of live shoots per pot remained approximately stable in both intact treatments (Figure 3.6). Shoot death and the emergence of new shoots were not recorded in the intact treatments. Therefore, we do not know the nature of the stability in shoot numbers. There are two possible causes for this stability. First, in the intact treatments only very few new shoots may have emerged, while shoot death was negligible. This would be a static stability. Second, the stability in shoot numbers might have been dynamic. In that case, many new shoots emerged, while existing shoots died at a similar rate. Shoot recovery was quite high in the clipped treatments. This shows that there was at least a potential for new shoot growth in the experimental pots. Therefore, the second explanation cannot be excluded.

The conditions for plant growth between the treatments differed considerably. Therefore, differences in new shoot growth between intact and clipped treatments can be expected. More new shoots may have emerged in the clipped treatments. By enhanced shoot growth in clipped pots, plants may achieve fast recovery of photosynthetic activity. On the other hand, fewer new shoots may have emerged in the clipped pots. The severe stress and nutrient loss by clipping might have reduced shoot growth. In future research it would be useful to record shoot death and the emergence of new shoots in all treatments. Thus, it will become possible to investigate whether there are differences in new shoot growth between intact and dry treatments. This might give insight in how shoot recovery works in clipped *Spartina anglica* plants. (I.e. is new shoot growth enhanced by clipping?).

There was a great difference in shoot recovery between the two clipped treatments. In five weeks, shoot numbers in the dry-clipped pots recovered to over 75% of initial shoot numbers. This strongly suggests that eventually clipped *Spartina anglica* plants will completely recover under dry conditions. Shoot recovery in the flooded-clipped pots was less than 30%. Thus, it appears that clipped *Spartina anglica* plants can not easily recover under flooded conditions. This idea is supported by Adams & Bate (1995). They found that the production of new shoots was reduced in submerged *Spartina maritima* plants. These authors suggested two possible causes for their results. First, the anoxic sediment conditions during flooding might inhibit stem production. Second, submerged plants might allocate more energy into stem elongation than into the production of new shoots. Thus, plants can emerge quickly so that photosynthesis will again become possible. In our experiment, probably both causes played a role.

## 4.2.2 Above- and below-ground biomass after treatments

### *Above-ground biomass*

There was almost no difference in live above-ground biomass between dry-intact and flooded-intact pots (Figure 3.7). This was also found for shoot numbers in section 4.2.1. Therefore, it appears that there was no flooding effect on intact *Spartina anglica* plants. In contrast, some studies found that growth in *Spartina* spp. was better under partly flooded or more reduced circumstances (Koch & Mendelssohn, 1989; Adams & Bate, 1995). The results in this experiment do not support these findings. However, dead above-ground biomass was significantly greater in dry-intact pots than in flooded-intact pots (Figure 3.8). Thus, more shoots may have died in dry-intact pots than in flooded-intact pots. This would indicate that *Spartina anglica* also preferably grows under wetter conditions. In this experiment however, shoot death was not recorded. Therefore, no conclusive remarks can be made on the differences in above-ground dead biomass between dry and flooded treatments.

Flooding had a large negative effect on live above-ground biomass in clipped plants. On average, live above-ground biomass in dry-clipped pots was more than twice as high than in flooded-clipped pots. Thus, either *Spartina anglica* recovery from clipping is not possible under flooded conditions, or recovery is much faster under dry conditions. The discussion in the following sections will show which of these possibilities is most probable.

### *Below-ground biomass*

Both flooding and clipping appeared to have negative effects on *Spartina anglica* live below-ground biomass (Figure 3.9). The combination of flooding and clipping had an extra strong negative effect. Dead below-ground biomass seemed higher in flooded pots than in dry pots (Figure 3.10). Thus, flooding did not only appear to reduce below-ground growth. Instead, flooding also seemed to cause higher death rates of roots and rhizomes. On average, the percentage of live material below ground was similar in all treatments except for the flooded-clipped pots (Figure 3.11). In most of the flooded-clipped pots the condition of roots and rhizomes was bad (Figure 3.12). Comparing individual flooded-intact pots with dry-clipped pots, it appears that flooding had a stronger negative effect on root condition than clipping.

### *Possible negative effects of clipping on below-ground biomass*

There are two possible negative effects of clipping on live below-ground biomass. First, the removal of shoots and leaves prevents the production of energy by photosynthesis. Thus, clipped plants have less energy to spend than intact plants. Any energy that can be spent, will probably be allocated to the growth of new shoots. Consequently, growth of roots and rhizomes will be less in clipped plants. Secondly, by removing all above-ground parts, oxygen transport to below-ground parts is no longer possible. Aerobic root respiration is known to be essential for plant growth and nutrient uptake. Therefore, many wetland species have evolved aerenchyma to supply the roots with oxygen (Burdick & Mendelssohn, 1990; Wijte & Gallagher, 1991; Arenovski & Howes, 1992). By cutting off the root oxygen supply through aerenchyma, the roots will suffer from oxygen depletion (Jordan & Whigham, 1988). This oxygen stress will reduce rhizome functioning and growth. Therefore, lack of oxygen seems the main cause of the lower values for live below-ground biomass in clipped pots. However, lack of energy from photosynthetic products can not be totally ruled out. Clipping, did not increase below-ground dead biomass compared to the corresponding intact treatments (Figure 3.10). Thus, clipping caused live below-ground biomass to be lower only by reducing growth of roots and rhizomes. The death rate of below-ground material was not directly affected by clipping.

### *Possible negative effects of flooding on below-ground biomass*

Flooding causes soils to become waterlogged and highly reduced. In reduced soils, anaerobic microbial by-products, that are often toxic can accumulate (Burdick & Mendelssohn, 1990; Webb *et al.*, 1995). One of these microbial by-products is the highly toxic sulphide ( $H_2S$ ). Sulphide affects growth negatively by decreasing the ability of nutrient uptake, decreasing oxygen availability and by metabolic toxicity (Howes *et al.*, 1981; DeLaune *et al.*, 1983; Koch & Mendelssohn, 1989). Sulphide may also cause death of roots and rhizomes. Koch & Mendelssohn (1989) found that  $H_2S$  caused soft rotted roots in *Spartina townsendii*. While extracting below-ground material from the pots, we observed that the soil cores differed in colour between the different treatments. The soil cores of flooded-clipped pots were predominantly black in colour and smelled strongly of sulphide. Many roots and rhizomes in these pots were rotten or had already completely decayed. In the other treatments, black spots of sulphide were also observed. However, these spots were much smaller and even hardly present in the dry-intact treatment. Dead roots and rhizomes were usually found in the black spots. Thus, in this experiment, accumulation of sulphide occurred. This was probably an important cause of the death of below-ground material. In flooded soils, oxygen diffuses approximately ten thousand times slower than in dry soils (Koch & Mendelssohn, 1989). Therefore, oxygen will sooner be a limiting factor in flooded pots than in dry pots. The effects of oxygen limitation will be further discussed in section 4.2.5.

#### **4.2.3 Regrowth of shoots in clipped plants**

##### *Emerging new shoots*

At the first monitoring date, the emergence of new shoots already differed between dry-clipped and flooded-clipped pots (Figure 3.13). This difference became greater in time. In dry-clipped pots, the number of new shoots increased in an almost linear fashion. We do not know how many new shoots emerged in the intact treatments. Thus, it is not known if new shoot growth is affected by clipping. However, only few new shoots died in the dry-clipped treatment. Therefore, it seems that clipping had no negative effect on the emergence of new shoots in dry-clipped pots. Consequently, under dry conditions new *Spartina anglica* shoots will probably survive and clipped plants can completely recover from clipping.

In flooded-clipped pots, there was a slight initial increase in emerging new shoots. However, soon many new shoots died in the flooded treatment. Thus, it appears that new shoots of clipped *Spartina anglica* plants can not survive under permanently flooded conditions. A possible cause for this effect is that shoots may die of energy shortage. Since all above-ground material was removed, energy rich photosynthates can no longer be produced. Consequently, there is not enough energy to sustain the new emerging shoots. As a result, these shoots may die shortly after they emerged. However, only few new shoots in the dry-clipped treatment died. The fact that these latter shoots are above water level should enable gas exchange and photosynthesis. Perhaps under dry conditions, these small new emerging shoots can already generate enough energy to survive. Furthermore in dry-clipped pots, new shoots might immediately play a significant role in oxygen transport to the roots. In this way, probably only minor amounts of oxygen can be transported. Nevertheless, the aerenchyma in these small shoots might supply sufficient oxygen to maintain the roots and rhizomes in good condition. In flooded-clipped pots, both photosynthesis and oxygen transport to below-ground parts is not possible. Hence, the general condition of *Spartina anglica* in this treatment can only deteriorate. In short, new shoots in the flooded-clipped treatments probably died since flooding caused energy shortage and a bad condition of roots and rhizomes (see section 4.2.2). The latter was mainly caused by oxygen stress and the accumulation of toxic compounds. This has been discussed in section 4.2.2 and will be further discussed in section 4.2.5.

### *Regrowth from clipped shoots*

At first, regrowth from clipped shoots did not differ between flooded and dry pots (Figure 3.14). In the end however, regrowth occurred in 47% of dry-clipped shoots and only in 28% of flooded-clipped shoots. Only 21% of the submerged regrowing shoots survived flooding. Thus, recovery from clipping seems much more difficult under flooded conditions. As with new shoots, this will probably be caused by oxygen stress and the bad conditions of roots and rhizomes in flooded-clipped pots.

The differences in regrowing shoot numbers between the two treatments, were lower than the differences in new shoot growth. This might indicate that flooded-clipped plants put more energy in regrowth from old shoots than in the production of new shoots. Another possibility is that regrowth from old shoots is more easy or costs less energy than the production of new shoots. In the pots, I found that new shoots were usually much shorter and had less leaf-surface than shoots that regrew from old shoots (personal observation). Thus, somehow the latter are able to grow higher in a similar amount of time. In flooded-clipped pots, shoots that regrew from old shoots were often able to protrude above water-level. This might be the main reason why relatively regrowth from old shoots was more successful than new shoot growth in flooded-clipped pots.

#### **4.2.4 Recovery of clipped shoots after long term flooding**

##### *Recovery of new emerging shoots*

After 35 days, new shoots emerged at approximately the same rate as before in the dry-clipped treatment (Figure 3.15). It appeared that the potential for new shoot growth had still not leveled off in this treatment. This indicates that *Spartina anglica* in the dry-clipped pots was in a good condition and that recovery was still in full progress.

After flooding had ceased, there was a fast increase in new shoot growth in previously flooded pots (Figure 3.15). However, this increase was mainly caused by new shoot growth in two pots (Appendix VI). Thus, only some pots could recover from long term flooding. These were pots that had a high number of regrowing shoots at the moment the water level was decreased. Therefore, it appears that only plants that produce enough shoots during flooding can survive when finally dry conditions have returned. All the pots that showed shoot recovery after flooding, had at least one regrowing shoot above water level when the conditions were still flooded. In pots that showed no recovery after flooding had ceased, no shoots were found above water level during flooding. Consequently, for the survival of clipped *Spartina anglica* plants it seems to be vitally important that there are shoots above water level. Survival in plants with shoots above water level will be better, since the below-ground parts can be supplied with oxygen through aerenchyma. The three flooded-clipped pots with the highest percentage of live material below ground, all had at least one shoot above water level during flooding. Most of the other pots had no shoots above water level (personal observation). Thus root condition is better when oxygen transport through aerenchyma is possible. The consequences of oxygen stress and anoxic root conditions will be further discussed in section 4.2.5.

### *Recovery of regrowing clipped shoots*

After flooding had ceased, no more regrowth occurred in clipped shoots (Figure 3.16). In both treatments, there was practically no increase in regrowing old shoots after three weeks. Therefore, it appears that regrowth from clipped shoots is only possible in the first weeks after clipping. After that, the cores will probably have died. In the dry treatment this might be caused by the drying out of cores. In the flooded treatment, this might be caused by rotting.

### **4.2.5 Soil-oxygen content**

Soil-oxygen content was low in all pots and did not differ between the four treatments (Figure 3.17). However, there was a great difference in shoot recovery between dry-clipped and flooded-clipped pots. Flooding also caused negative effects on roots and rhizomes. It is known that soil inundation drastically affects gas exchange in both plants and soil (Armstrong *et al.*, 1985). Soil redox and oxygen availability decrease under flooded conditions (Burdick & Mendelssohn, 1990; Webb *et al.*, 1995). This suggests that there must have been differences in soil oxygen content between the four treatments. The major differences in soil oxygen content probably occurred in the root zone. Wetland grasses can oxidise sediments in their root zone (Howes *et al.*, 1981). In our soil samples, we observed red patches of oxidised iron in areas with a high density of roots and rhizomes. Most of these patches were found in dry-intact pots. In flooded-clipped pots, we found no traces of oxidised iron. We did find large areas of blackened soil in the flooded-clipped pots, indicating the presence of sulphide (see section 4.2.2). Thus it appears that in flooded-clipped pots the soil was more reduced than in the other treatments.

The method we used for determining oxygen content was not precise enough to distinguish differences in oxygen content between micro-sites. Therefore, oxygen content in the rhizosphere could not be measured. Considering our observations, it is highly probable that there were distinct differences in rhizosphere oxygen content between the treatments. To quantify oxygen availability to saltmarsh plants, a method should be found that can measure oxygen content in the rhizosphere.

### *Consequences of low soil oxygen contents*

Saltmarsh soils and soils beneath *Spartina* swards are highly reduced and high in sulphides (Howes *et al.*, 1981; Armstrong *et al.*, 1985). Such soil conditions can have strong negative effects on plant growth. Growth, as a function of nitrogen-uptake, is strongly influenced by the oxygen availability to the roots (Mendelssohn & McKee, 1988; Arenovski & Howes, 1992). It is found that plant nitrogen uptake decreases under hypoxia and is strongly inhibited by even low concentrations of sulphide (Bradley, 1990; Webb *et al.*, 1995). Nitrogen is known to be the most important limiting nutrient in saltmarshes (Smart & Barko, 1980; Webb *et al.*, 1995).

Since *Spartina anglica* needs high amounts of nitrogen for growth (van Schreven, 1958), reduced soil conditions will cause limited productivity and growth in *Spartina anglica*. Soil conditions are even worse for flooded plants. Therefore, plant growth will be negatively affected by flooding. Ellison *et al.* (1986) found that total above- and below-ground production of *Spartina alterniflora* decreased with tidal height. Flooding causes saltmarsh soils to become even more reduced and can result in sulphide accumulation and increased root oxygen deficiencies (Mendelssohn & McKee, 1988). Accumulated sulphide is highly toxic and inhibits root production (Delaune *et al.*, 1983). In an experiment, Koch & Mendelssohn (1989) found that below-ground biomass of *Spartina alterniflora* decreased in soils containing sulphide. Thus, under flooded conditions, the roots and rhizomes of saltmarsh plants are surrounded by a very hostile environment. Therefore, saltmarsh plants have evolved a well developed aerenchyma.

The aerenchyma provides a pathway to diffusion and sometimes for bulk flow of oxygen to roots (Jordan & Whigham, 1988). The presence of oxygen in roots supports respiration and may leak into the rhizosphere. Consequently, nutrient availability is enhanced and anaerobic phytotoxins can be eliminated (Jordan & Whigham, 1988, Koch & Mendelssohn, 1989).

In the previous paragraph, it has become clear that saltmarsh plants greatly depend on aerenchyma for their survival. Oxygen transport through aerenchyma enables the plants to create favourable soil conditions. The results in this experiment support the idea that aerenchyma is vitally important for *Spartina anglica*. We found practically no differences between the two intact treatments. The only significant difference we found between dry-intact and flooded-intact pots, was that live below-ground biomass was slightly lower in flooded-intact pots. This indicates that for *Spartina anglica* soil conditions are worse during flooding, probably due to sulphide accumulation and the lower rate of oxygen diffusion in the soil during flooding. Clipping of *Spartina anglica* had only distinct negative and lethal effects in flooded-clipped pots that had no shoots above water level. Thus, it appears that *Spartina anglica* can survive under highly reduced soil conditions, as long as gas exchange between above- and below-ground parts remains possible.

### 4.3 Implications for the field

The greenhouse experiment revealed that *Spartina anglica* suffered most from the effects of shoot removal in flooded areas. In these areas, toxic microbial by-products accumulate, which can only be eliminated by active oxygen transport to the root zone. Plants that had their shoots removed, will be unable to oxidise their root zone. Consequently, these plants might die from oxygen stress and sulphide toxicity. In the field, we found that Greylags grubbed for *Spartina anglica* rhizomes especially in the flooded areas. This means that foraging Greylags could potentially be devastating to large parts of the *Spartina anglica* stand on the island of Schiermonnikoog. In field studies, it has often been found that grazing of geese on below-ground plant parts drastically decreases the vegetation cover in tidal *Spartina* and *Scirpus* marshes (Giroux & Bédard, 1987a; Bélanger & Bédard, 1994a; Esselink *et al.*, 1997). In an experiment, Giroux and Bédard (1987b) found that simulated goose grubbing had negative effects on all growth characteristics of *Scirpus*. The negative effects of goose grubbing seem to be most severe when there is an interaction with another, usually abiotic, factor. For example, Iacobelli and Jefferies (1991) found that increased salt concentrations prevented plant regrowth at grubbed sites. Furthermore, Esselink *et al.* (1997) found that grubbed plants failed to regenerate when they were subject to wave exposure. Finally, the results in this study indicate that grubbed *Spartina anglica* can not recover in combination with flooding. Goose grubbing is highly stressful for salt-marsh plants. Increased salt concentration, wave exposure and flooding are probably also stressful circumstances. Thus, possibly salt marsh plants can only overcome the severe stress of goose grubbing if they are not simultaneously exposed to another stressor. This leads to the conclusion that, salt-marsh vegetation will fail to regenerate in grubbed areas where there is an interaction with a stressful environmental factor.

Iacobelli and Jefferies (1991) and Miller *et al.* (1996) found that salt-marsh vegetation failed to regenerate in areas of severe exploitation by geese. On Schiermonnikoog however, goose feeding pressure on *Spartina anglica* was very low in the winter of 1995-1996. In section 4.1, I showed that the extremely long frost period might have had a part in that. Most important, however, is the fact that *Scirpus maritimus* tubers seemed to be the main food source of wintering Greylags on Schiermonnikoog. At the moment, Greylags probably consider *Spartina anglica* rhizomes only as a kind of food supplement. Consequently, it can not be expected that on short term Goose feeding pressure on *Spartina anglica* will dramatically increase. Only when the wintering Greylag Goose population on the island of Schiermonnikoog increases rapidly in the coming years a higher feeding pressure can be expected. However, the more intense goose foraging on *Scirpus maritimus* tubers might cause a strong decrease in the *Scirpus maritimus* stand on the island. The *Scirpus maritimus* stand may also decrease due to successional changes in the brackish marsh. In the future, *Scirpus maritimus* might be replaced by *Phragmites australis*. When in the long turn the *Scirpus* marsh has been depleted to the level that goose foraging will no longer be profitable, the Greylags might either stop using Schiermonnikoog as a winter staging area or shift their diet to *Spartina anglica* rhizomes. When *Spartina anglica* will become the main food source, goose grubbing in the salt marsh will greatly intensify and parts of the *Spartina anglica* stand on Schiermonnikoog might disappear.

## ACKNOWLEDGMENTS

I have been very fortunate in having had the best field work colleagues that can be imagined, Liesbeth Bakker and Aaldrik Pot. Their hard work, incessant enthusiasm and great personalities guaranteed a more than pleasant working atmosphere and excellent team work and makes me have warm memories of our stay on an otherwise freezing Schiermonnikoog. I compliment Tom for having the courage to leave the comfort and sterility of his molecular lab to help us determine vegetation cover on the slippery, muddy salt marsh in the pouring rain. Many thanks for Harm van Wijnen who helped me with the elevation measurements in the transect and who refreshed my memory on how to work with the necessary equipment. Rudy van Diggelen briefly introduced me to IDRISI, without which the vegetation maps could not have been made. With respect to the greenhouse experiment, I am grateful to the Department of Plant Physiology for allowing me some space in one of their greenhouses. Iris van Duren kindly provided me with electrodes for soil-redox measurements in my experimental pots and explained how they worked. Unfortunately, the redox measurements turned out to be complete and utter gibberish so I have not incorporated them in this report. I am indebted to the people of the chemical lab of the Department of Plant Ecology who occasionally took care of the experimental plants and provided me with the means to determine soil redox and plant biomass. I thank the people from the Department of Microbial Ecology for providing the chemicals to calibrate the redox electrodes, for all their instructions and for letting me use their oxygen measuring equipment. Finally and most importantly, I owe a lot of thanks to my supervisors, Peter Esselink and René van der Wal. They have helped me in many, many ways with all stages of this research project. I have learned a lot from their good advice and healthy criticism and will always remember their enthusiasm for the project and their patience and great moral support in one of the hardest times I have had so far.

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Appendix I

Marsh elevation (m above N.A.P.) measured in the transect to create Figure 3.1

distance	Distance (in m) from the north-western corner in the transect																	
	5	15	25	35	45	55	65	75	85	95	105	115	125	135	145	155	165	175
5	1.32	1.32	1.33	1.39	1.36	1.43	1.45	1.40	1.41	1.49	1.48	1.41	1.43	1.45	1.38	1.38	1.22	1.28
15	1.38	1.37	1.42	1.46	1.45	1.37	1.41	1.47	1.39	1.47	1.41	1.33	1.42	1.39	1.37	1.36	1.29	1.29
25	1.31	1.35	1.42	1.39	1.44	1.37	1.37	1.23	1.36	1.42	1.39	1.38	1.31	1.24	1.35	1.37	1.29	1.30
35	1.37	1.34	1.40	1.39	1.38	1.37	1.32	1.38	1.36	1.32	1.29	1.35	1.37	1.33	1.29	1.31	1.30	1.35
45	1.34	1.24	1.28	1.37	1.30	1.35	1.41	1.37	1.39	1.34	1.22	1.25	1.35	1.36	1.35	1.34	1.19	1.22
55	1.31	1.12	1.28	1.31	1.32	1.21	1.34	1.33	1.24	1.35	1.37	1.17	1.28	1.31	1.34	1.32	1.33	1.31
65	1.18	1.15	1.27	1.32	1.34	1.34	1.28	1.34	1.32	1.26	1.32	1.33	1.33	1.32	1.38	1.32	1.27	1.31
75	1.30	1.29	1.29	1.30	1.32	1.32	1.33	1.34	1.36	1.32	1.37	1.32	1.35	1.34	1.31	1.34	1.33	1.30
85	1.30	1.30	1.21	1.30	1.32	1.35	1.20	1.17	1.32	1.28	1.35	1.34	1.31	1.33	1.33	1.32	1.33	1.30
95	1.28	1.33	1.33	1.32	1.37	1.41	1.22	1.33	1.35	1.35	1.34	1.33	1.36	1.35	1.34	1.34	1.33	1.33
105	1.32	1.30	1.34	1.09	1.15	1.36	1.38	1.37	1.38	1.35	1.35	1.34	1.28	1.24	1.31	1.21	1.25	1.23
115	1.26	1.32	1.33	1.35	1.34	1.29	1.24	1.32	1.31	1.37	1.18	1.30	1.26	1.27	1.25	1.30	1.25	1.18
125	1.33	1.12	1.31	1.33	1.31	1.30	1.20	1.33	1.17	1.16	1.17	1.17	1.27	1.31	1.30	1.31	1.31	1.36
135	1.16	1.30	1.17	1.20	1.19	1.23	1.18	1.22	1.22	1.17	1.21	1.14	1.31	1.19	1.38	1.35	1.36	1.21
145	1.19	1.19	1.20	1.28	1.17	1.20	1.21	1.21	1.25	1.19	1.19	1.16	1.18	1.18	1.33	1.33	1.39	1.36
155	1.22	-	1.32	-	1.22	-	1.23	-	1.21	-	1.19	-	1.22	-	1.17	-	1.26	-
175	1.21	-	1.24	-	1.25	-	1.25	-	1.22	-	1.24	-	1.22	-	1.22	-	1.22	-
195	1.21	-	1.23	-	1.22	-	1.24	-	1.25	-	1.24	-	1.22	-	1.26	-	1.21	-
215	1.21	-	1.22	-	1.21	-	1.21	-	1.22	-	1.22	-	1.23	-	1.19	-	1.18	-
235	1.16	-	1.18	-	1.17	-	1.17	-	1.24	-	1.21	-	1.27	-	1.24	-	1.17	-
255	1.11	-	1.17	-	1.21	-	1.22	-	1.21	-	1.19	-	1.19	-	1.11	-	1.13	-
275	1.09	-	1.10	-	1.13	-	1.09	-	1.08	-	1.11	-	1.14	-	1.08	-	1.11	-
295	1.10	-	1.29	-	1.08	-	1.08	-	1.09	-	1.10	-	1.08	-	1.07	-	1.05	-
315	1.13	-	1.09	-	1.10	-	1.11	-	1.10	-	1.10	-	1.07	-	1.06	-	1.00	-
335	1.13	-	1.11	-	1.11	-	1.12	-	1.12	-	1.10	-	1.07	-	1.02	-	1.03	-
355	1.14	-	1.15	-	1.14	-	1.13	-	1.11	-	1.09	-	1.02	-	1.02	-	1.04	-
375	1.12	-	1.10	-	1.13	-	1.08	-	1.16	-	1.13	-	1.04	-	0.99	-	0.97	-
395	1.07	-	1.09	-	1.08	-	1.07	-	1.09	-	1.05	-	1.04	-	1.01	-	1.07	-
415	1.13	-	1.13	-	1.13	-	1.06	-	1.05	-	1.07	-	1.01	-	1.00	-	1.00	-
435	1.10	-	1.11	-	1.11	-	1.07	-	1.05	-	1.04	-	1.02	-	1.01	-	1.00	-
455	1.09	-	1.06	-	1.08	-	1.05	-	1.03	-	1.04	-	1.06	-	0.99	-	1.00	-
475	1.18	-	1.17	-	1.09	-	1.06	-	1.04	-	1.04	-	1.03	-	1.01	-	1.01	-
495	0.98	-	1.12	-	1.10	-	1.06	-	1.06	-	1.06	-	1.04	-	1.03	-	1.05	-
515	1.18	-	1.12	-	1.09	-	1.08	-	1.06	-	1.06	-	1.05	-	1.05	-	1.01	-
535	1.18	-	1.13	-	1.10	-	1.04	-	1.05	-	1.14	-	1.09	-	1.01	-	1.02	-
555	1.14	-	1.10	-	1.07	-	1.06	-	1.10	-	1.07	-	1.13	-	1.03	-	1.08	-
575	1.15	-	1.14	-	1.11	-	1.07	-	1.07	-	1.05	-	1.06	-	1.08	-	1.07	-
595	1.15	-	1.13	-	1.09	-	1.08	-	1.07	-	1.05	-	1.06	-	1.04	-	1.04	-
615	1.04	-	1.06	-	1.03	-	0.98	-	0.95	-	0.93	-	0.90	-	0.92	-	0.90	-
635	1.10	-	1.09	-	1.07	-	1.07	-	1.02	-	0.98	-	0.97	-	0.93	-	0.94	-
655	1.07	-	1.06	-	0.97	-	1.03	-	1.04	-	0.98	-	0.99	-	0.98	-	0.97	-
675	1.10	-	0.98	-	1.07	-	1.05	-	1.07	-	0.99	-	1.02	-	0.97	-	0.84	-
695	1.01	-	1.10	-	1.02	-	1.03	-	1.07	-	1.06	-	1.00	-	0.95	-	0.99	-
715	0.95	-	0.98	-	0.97	-	1.04	-	0.95	-	1.04	-	0.98	-	0.95	-	0.96	-
735	0.95	-	0.94	-	1.02	-	0.97	-	0.98	-	0.95	-	0.95	-	0.92	-	0.93	-
755	0.93	-	0.92	-	0.86	-	0.86	-	0.85	-	0.85	-	0.88	-	0.83	-	0.85	-
775	0.83	-	0.85	-	0.82	-	0.83	-	0.84	-	0.84	-	0.82	-	0.81	-	0.80	-
795	0.80	-	0.80	-	0.81	-	0.83	-	0.81	-	0.79	-	0.78	-	0.76	-	0.77	-

## Appendix II

**Clay thickness (cm) measured along the most western edge in the transect**

Distance from N-edge of the transect (m)	Clay thickness (cm)	Distance from N-edge of the transect (m)	Clay thickness (cm)
10	21	340	15
20	16	360	18
30	19	380	16
40	16	400	14
50	21	420	17
60	22	440	15
70	16	460	10
80	18	480	9
90	22	500	7
100	20	520	17
110	22	540	23
120	23	560	19
130	21	580	18
140	17	600	16
150	18	620	18
160	19	640	18
180	16	660	11
200	21	680	12
220	14	700	6
240	17	720	4
260	18	740	0.5
280	16	760	0.3
300	14	780	0.2
320	13	800	0.2

Appendix III

All data on individually marked *Spartina anglica* shoots

shoot number	position in clone	shoot height (cm)	date of disappearance	shoot number	position in clone	shoot height (cm)	date of disappearance
1	free	34	-	49	in clone	63	-
2	free	53	-	50	in clone	75	-
3	free	59	-	51	clone edge	45	-
4	clone edge	58	-	52	free	43	-
5	in clone	58	-	53	clone edge	60	-
6	free	35	-	54	in clone	50	-
7	clone edge	60	-	55	in clone	65	-
8	clone edge	33	-	56	clone edge	57	-
9	in clone	76	-	57	in clone	60	-
10	clone edge	74	-	58	free	55	-
11	in clone	92	-	59	clone edge	50	-
12	free	53	-	60	in clone	73	-
13	free	63	-	61	free	70	-
14	free	53	-	62	clone edge	68	-
15	clone edge	60	-	63	in clone	63	-
16	clone edge	57	-	64	clone edge	55	-
17	in clone	65	-	65	free	60	-
18	clone edge	32	-	66	clone edge	56	-
19	free	54	-	67	in clone	79	-
20	in clone	50	-	68	free	62	-
21	free	54	-	69	clone edge	62	-
22	in clone	69	-	70	in clone	70	-
23	free	45	27-11-1995	71	clone edge	66	-
24	free	55	27-11-1995	72	free	55	-
25	clone edge	59	-	73	in clone	79	-
26	in clone	53	-	74	free	76	-
27	free	59	-	75	clone edge	74	-
28	in clone	78	-	76	free	40	-
29	clone edge	73	-	77	in clone	75	-
30	free	49	-	78	clone edge	77	-
31	in clone	72	-	79	free	54	-
32	free	52	-	80	free	60	-
33	free	67	-	81	in clone	71	-
34	clone edge	62	-	82	clone edge	71	-
35	clone edge	73	-	83	clone edge	59	-
36	free	53	23-11-1995	84	free	49	-
37	clone edge	80	-	85	free	59	-
38	free	59	-	86	clone edge	82	-
39	in clone	94	-	87	in clone	72	-
40	clone edge	59	-	88	free	59	-
41	free	53	-	89	clone edge	52	-
42	clone edge	54	-	90	free	62	-
43	clone edge	55	-	91	free	72	-
44	clone edge	57	-	92	clone edge	52	-
45	clone edge	68	-	93	in clone	62	-
46	free	67	-	94	free	46	-
47	free	61	21-11-1995	95	free	60	-
48	clone edge	80	-	96	clone edge	80	-

### Appendix III

shoot number	position in clone	shoot height (cm)	date of disappearance	shoot number	position in clone	shoot height (cm)	date of disappearance
97	in clone	62	-	147	free	57	-
98	in clone	81	-	148	in clone	86	-
99	free	61	-	149	free	61	24-11-1995
100	clone edge	73	-	150	clone edge	72	-
101	free	52	-	151	in clone	66	-
102	clone edge	56	-	152	clone edge	88	-
103	in clone	55	-	153	free	50	23-11-1995
104	free	59	-	154	in clone	74	-
105	clone edge	60	-	155	free	60	29-11-1995
106	in clone	79	-	156	clone edge	72	-
107	free	30	-	157	in clone	75	-
108	clone edge	62	-	158	clone edge	55	-
109	in clone	64	-	159	free	45	-
110	free	56	-	160	free	65	-
111	clone edge	55	-	161	in clone	80	-
112	in clone	87	-	162	clone edge	68	-
113	free	54	-	163	in clone	65	-
114	clone edge	66	-	164	free	54	13-11-1995
115	in clone	81	-	165	clone edge	80	-
116	free	36	-	166	free	63	-
117	clone edge	62	-	167	free	38	-
118	in clone	73	-	168	clone edge	65	-
119	free	53	-	169	in clone	58	-
120	clone edge	79	-	170	free	70	-
121	in clone	59	-	171	free	79	-
122	free	35	-	172	clone edge	75	-
123	clone edge	53	-	173	in clone	90	-
124	in clone	53	-	174	free	72	29-11-1995
125	free	52	-	175	clone edge	75	-
126	clone edge	56	-	176	in clone	76	-
127	in clone	64	-	177	free	58	-
128	free	48	16-11-1995	178	clone edge	80	-
129	clone edge	71	-	179	in clone	80	-
130	in clone	81	-	180	free	56	-
131	clone edge	78	-	181	clone edge	52	-
132	in clone	75	-	182	in clone	73	-
133	free	62	27-11-1995	183	free	71	-
134	clone edge	58	-	184	clone edge	68	-
135	in clone	67	-	185	in clone	70	-
136	free	63	13-11-1995	186	clone edge	62	-
137	free	57	24-11-1995	187	in clone	77	-
138	clone edge	58	-	188	free	59	23-11-1995
139	in clone	85	-	189	free	68	29-11-1995
140	free	63	-	190	clone edge	87	-
141	clone edge	75	-	191	in clone	72	-
142	in clone	77	-	192	free	73	29-11-1995
143	free	52	-	193	clone edge	53	-
144	clone edge	75	-	194	in clone	86	-
145	in clone	70	-	195	free	66	-
146	clone edge	55	-	196	clone edge	66	-

## Appendix IV

### Vegetation cover of all species other than *Spartina anglica*

#### Vegetation maps

- <i>Artemisia maritima</i>	48
- <i>Aster tripolium</i>	48
- <i>Atriplex portulacoides</i>	49
- <i>Atriplex prostrata</i>	49
- <i>Elymus athericus</i>	50
- <i>Festuca rubra</i>	50
- <i>Glaux maritima</i>	51
- <i>Limonium vulgaris</i>	51
- <i>Plantago maritima</i>	52
- <i>Puccinellia maritima</i>	52
- <i>Salicornia spec.</i>	53
- <i>Spergularia maritima</i>	53
- <i>Suaeda maritima</i>	54
- <i>Triglochin maritima</i>	54

#### Remaining species

Table IV. Occurrence of plant species that were found in less than 20 grid cells in the transect. Shown is the vegetation cover in percentage, the distance from the north edge of the transect and the number of 10 m x 10 m grid cells in which these species were found.

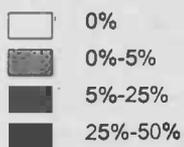
Species	cover	distance from N-border	# grid cells
Agrostis stolonifera	0-5%	30 m	2
Armeria maritima	0-5%	80 m	1
" "	0-5%	350 m	1
Juncus gerardii	0-5%	30 m	2
Juncus maritimus	0-5%	40 m	2
" "	0-5%	110m	1

Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Artemisia maritima*

*Aster tripolium*

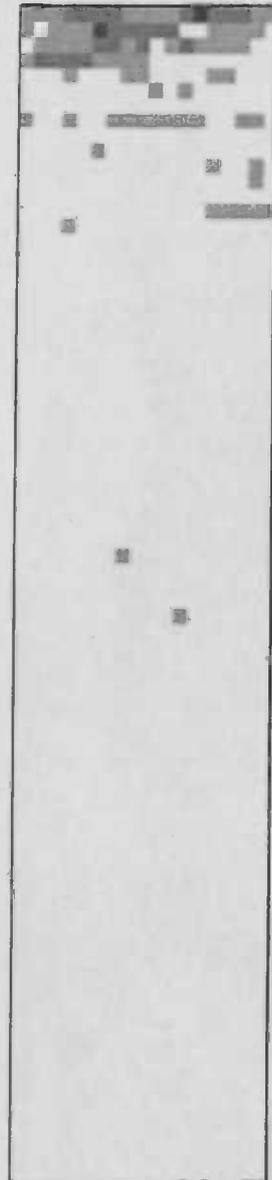
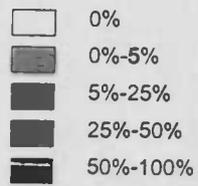


Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Atriplex portulacoides*

*Atriplex prostrata*

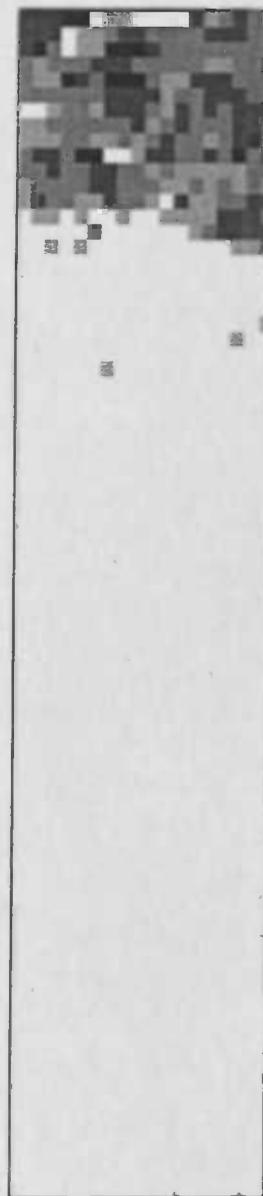
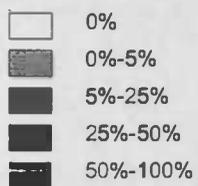
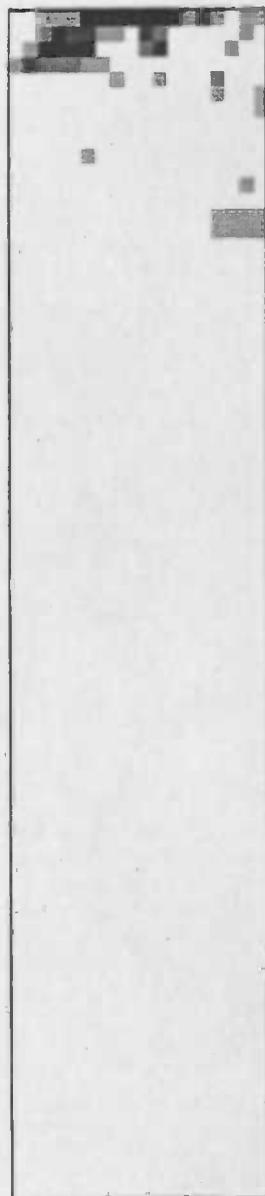


## Appendix IV

### Vegetation cover of all species other than *Spartina anglica*

*Elymus athericus*

*Festuca rubra*

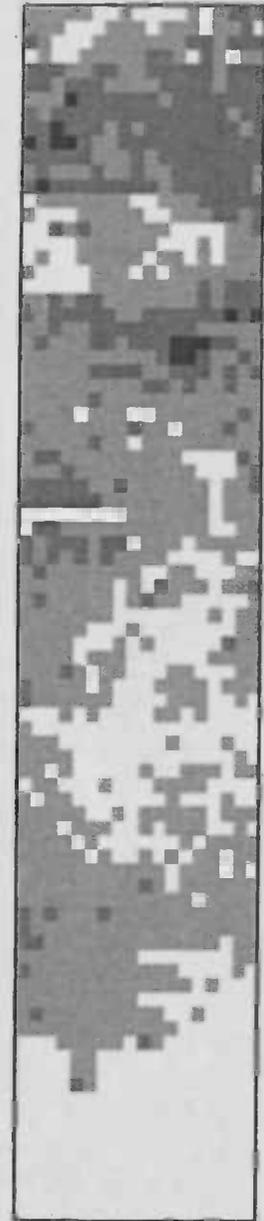
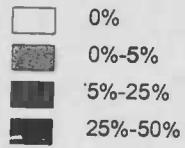
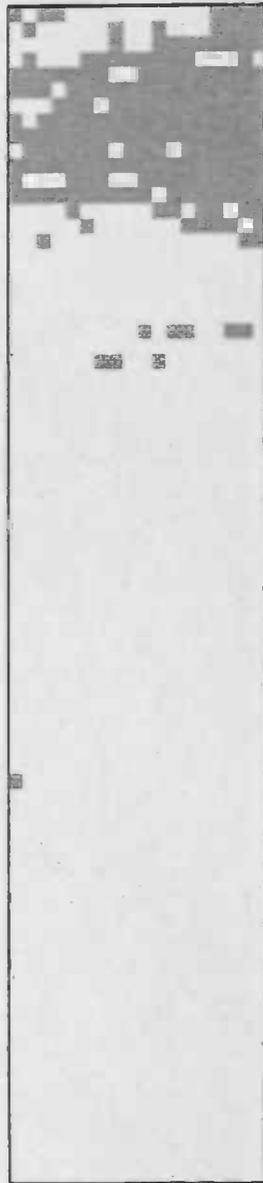


Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Glaux maritima*

*Limonium vulgaris*

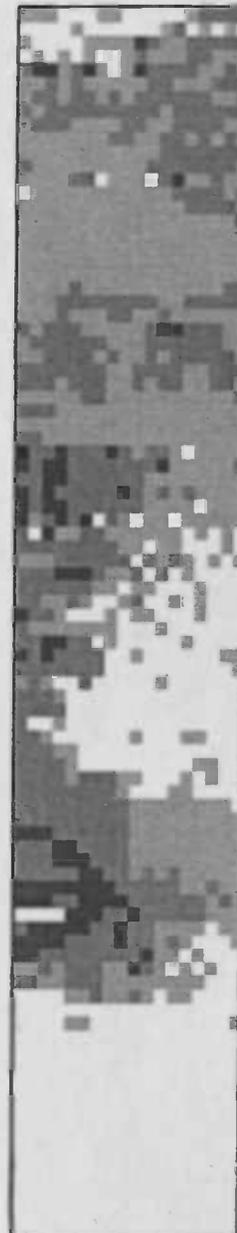
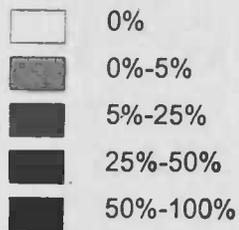
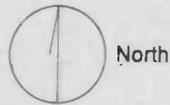
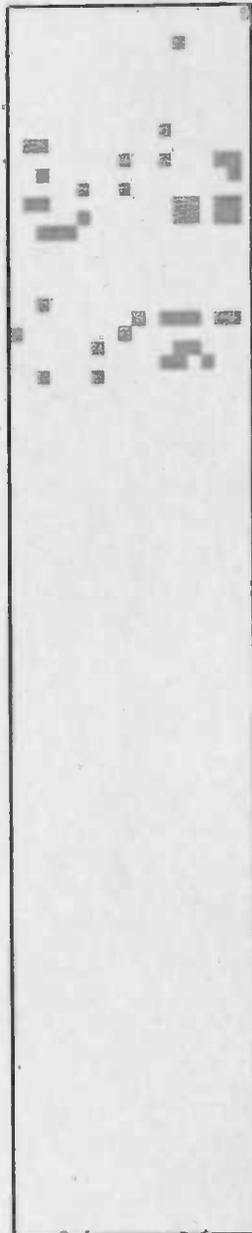


Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Plantago maritima*

*Puccinellia maritima*

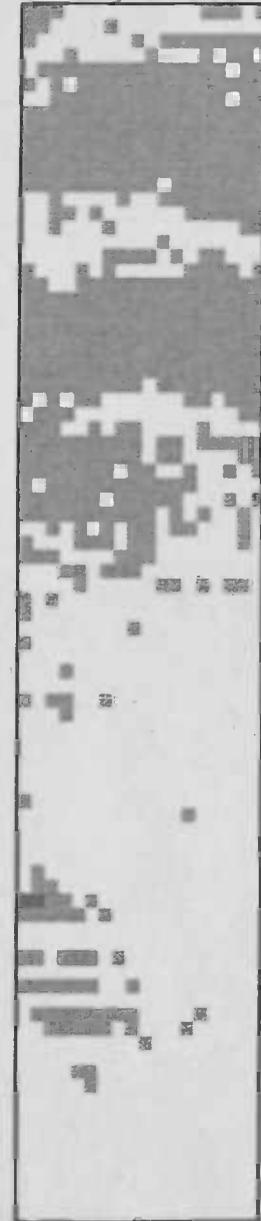
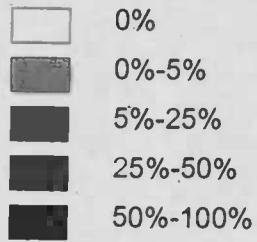
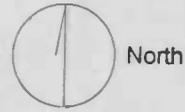
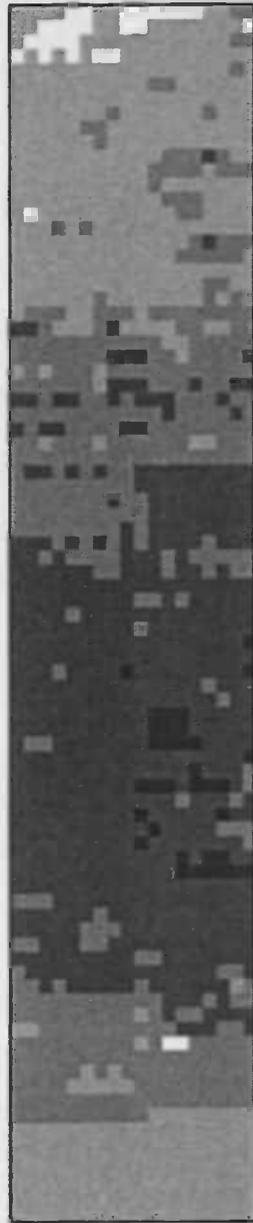


Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Salicornia spec.*

*Spergularia maritima*

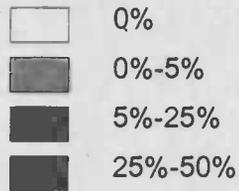
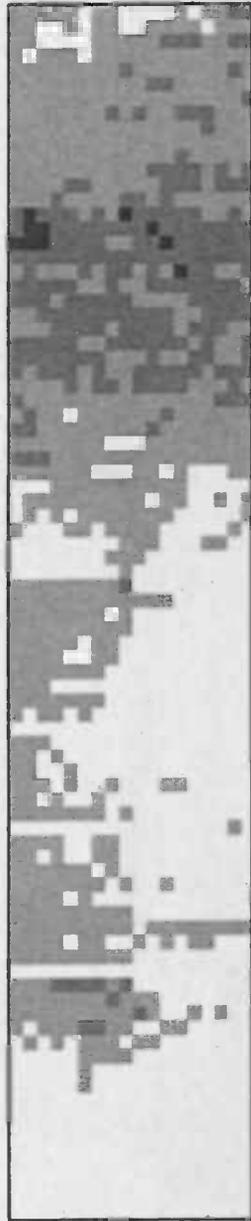


Appendix IV

Vegetation cover of all species other than *Spartina anglica*

*Suaeda maritima*

*Triglochin maritima*



Appendix V

All data on biomass determination and shoot counts

intact pots

clipped pots

	pot	biomass (g)		percentage live below	number of shoots	
		above	below		29-1	5-3
<b>D R Y  T R E A T M E N T</b>	1	-	-	-	6	8
	2	-	-	-	11	13
	3	-	-	-	19	23
	4	-	-	-	12	14
	5	-	-	-	9	13
	6	-	-	-	14	17
	7	-	-	-	7	14
	8	-	-	-	14	17
	9	-	-	-	16	22
	10	-	-	-	25	23
	11	4.66	7.23	64	18	21
	12	6.34	6.62	64	18	17
	13	5.3	13.2	86	22	30
	14	5.15	9.65	79	24	32
	15	7.33	9.58	73	27	28
	16	3.28	4.39	40	11	12
	17	3.36	2.07	60	6	12
	18	9.41	10.2	80	16	26
	19	3.16	5.53	45	16	19
	20	5.26	9.12	58	26	24
	21	4.11	6.17	69	21	27
<b>F L O O D E D  T R E A T M E N T</b>	1	-	-	-	23	27
	2	-	-	-	24	22
	3	-	-	-	10	12
	4	-	-	-	10	13
	5	-	-	-	7	12
	6	-	-	-	18	15
	7	-	-	-	18	21
	8	-	-	-	13	19
	9	-	-	-	20	21
	10	-	-	-	17	16
	11	4.16	4.72	57	24	20
	12	5.44	6.95	67	14	18
	13	6.5	7.69	44	26	22
	14	6.73	5.81	53	14	18
	15	7.29	9.25	65	25	24
	16	5.44	4.67	49	13	15
	17	3.22	4	55	9	14
	18	3.94	3.87	36	15	16
	19	1.27	3.33	30	16	18
	20	3.5	5.1	65	8	11
	21	5.06	6.08	72	10	15

	pot	biomass (g)		percentage live below	number of shoots	
		above	below		29-1	5-3
<b>D R Y  T R E A T M E N T</b>	1	-	-	-	17	10
	2	-	-	-	13	10
	3	-	-	-	17	10
	4	-	-	-	29	24
	5	-	-	-	7	6
	6	-	-	-	13	16
	7	-	-	-	7	7
	8	-	-	-	14	13
	9	-	-	-	13	5
	10	-	-	-	16	9
	11	0.31	5.28	74	9	7
	12	0.2	4.7	74	12	8
	13	0.79	4.17	66	15	14
	14	0.8	6.49	75	10	11
	15	0.84	4.04	68	17	11
	16	1.06	3.97	46	17	11
	17	0.56	3.23	51	15	10
	18	0.89	5.45	77	15	16
	19	0.18	5.74	79	16	10
	20	0.63	6.72	70	19	12
	21	1.97	8.43	75	23	22
<b>F L O O D E D  T R E A T M E N T</b>	1	-	-	-	14	2
	2	-	-	-	16	11
	3	-	-	-	12	2
	4	-	-	-	15	0
	5	-	-	-	26	14
	6	-	-	-	11	1
	7	-	-	-	9	2
	8	-	-	-	15	7
	9	-	-	-	11	3
	10	-	-	-	22	7
	11	0	0.17	3	7	0
	12	0.24	1.77	23	20	5
	13	0.19	1.54	16	20	4
	14	0.43	1.65	23	26	8
	15	0.21	0.78	12	26	4
	16	0	1.44	45	9	0
	17	0.07	0.55	7	12	3
	18	1.03	5.13	64	39	15
	19	1.17	3.77	63	16	11
	20	0.19	2.91	64	8	1
	21	0.08	0.7	16	12	1

Appendix VI

All data on emerging shoots in the clipped pots

	pot	monitoring dates																				
		Emerging new shoots											initial # of shoots	Regrowing clipped shoots								
		2-2	5-2	8-2	15-2	20-2	22-2	27-2	4-3	8-3	15-3	22-3		2-2	8-2	15-2	22-2	27-2	4-3	8-3	15-3	22-3
<b>D R Y  T R E A T M E N T</b>	1	2	1	1	1	1	1	1	1	1	1	2	17	0	6	8	8	9	9	9	9	9
	2	5	5	5	5	6	6	6	6	6	6	6	13	0	9	4	4	4	4	4	4	4
	3	2	3	2	3	2	2	3	3	3	3	3	17	0	7	7	7	7	7	7	7	7
	4	3	5	5	6	6	9	9	9	9	10	10	29	0	7	12	14	15	15	15	15	15
	5	2	3	4	4	4	4	4	5	5	5	5	7	0	1	1	1	1	1	1	1	1
	6	4	4	5	7	8	9	10	10	10	9	9	13	0	3	5	6	6	6	6	6	6
	7	1	1	1	1	1	1	1	1	1	2	3	7	0	2	6	6	6	6	6	6	6
	8	0	1	1	1	2	2	2	2	3	4	5	14	2	10	10	11	11	11	11	11	11
	9	3	3	3	3	2	2	2	2	2	2	3	13	0	2	2	3	3	3	3	3	3
	10	2	2	2	2	2	2	3	4	4	4	4	16	0	4	5	5	5	5	5	5	5
	11	2	2	2	3	3	3	3	3	-	-	-	9	0	1	3	4	4	4	-	-	-
	12	1	1	1	1	2	2	3	4	-	-	-	12	0	2	3	4	4	4	-	-	-
	13	2	2	2	4	4	4	5	6	-	-	-	15	0	5	8	8	8	8	-	-	-
	14	3	5	5	5	5	5	5	6	-	-	-	10	0	3	5	5	5	5	-	-	-
	15	1	1	2	3	4	4	4	4	-	-	-	17	0	6	7	7	7	7	-	-	-
	16	1	1	1	1	2	2	2	2	-	-	-	17	0	7	9	9	9	9	-	-	-
	17	1	1	1	1	1	1	2	2	-	-	-	15	0	5	8	8	8	8	-	-	-
	18	6	8	10	10	11	11	11	11	-	-	-	15	0	4	5	5	5	5	-	-	-
	19	0	0	0	0	1	1	2	3	-	-	-	16	0	3	3	5	6	7	-	-	-
	20	4	4	3	3	4	4	4	4	-	-	-	19	0	7	7	8	8	8	-	-	-
	21	1	1	2	3	2	2	3	4	-	-	-	23	0	16	16	18	18	18	-	-	-
<b>F L O O D E D  T R E A T M E N T</b>	1	1	1	1	0	0	0	0	0	0	1	14	0	2	3	2	2	2	2	2	2	
	2	0	1	1	2	2	2	2	2	3	8	9	16	0	5	7	10	9	9	10	10	10
	3	4	3	2	0	1	1	1	1	1	1	1	12	0	1	2	1	1	1	1	1	1
	4	0	1	2	2	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0
	5	2	2	2	2	1	1	1	1	1	2	6	26	0	9	11	12	12	13	14	14	14
	6	1	1	1	1	1	1	0	0	0	0	0	11	0	1	1	1	1	1	1	1	1
	7	1	1	1	0	0	0	0	0	0	0	0	9	0	3	2	2	2	2	2	1	1
	8	3	3	2	2	1	1	1	2	3	4	4	15	0	3	4	4	4	4	4	4	4
	9	0	0	0	0	0	0	0	0	0	0	0	11	0	3	4	4	4	2	2	2	2
	10	1	1	1	1	0	0	0	0	0	0	1	22	0	3	6	8	8	7	7	7	7
	11	0	0	0	0	0	0	0	0	-	-	-	7	0	2	0	0	0	0	-	-	-
12	2	2	1	1	2	1	1	1	-	-	-	20	0	7	8	4	4	4	-	-	-	
13	1	1	1	2	2	3	2	1	-	-	-	20	0	5	5	4	3	3	-	-	-	
14	2	3	3	2	3	2	2	2	-	-	-	26	0	6	8	7	6	6	-	-	-	
15	1	1	0	0	0	0	0	0	-	-	-	26	0	4	4	4	4	4	-	-	-	
16	0	0	0	0	0	0	0	0	-	-	-	9	0	1	0	0	0	0	-	-	-	
17	2	2	1	1	1	1	1	1	-	-	-	12	0	3	2	2	2	2	-	-	-	
18	2	3	5	4	3	3	4	3	-	-	-	39	0	10	12	13	13	12	-	-	-	
19	1	1	1	2	1	1	1	1	-	-	-	16	0	7	8	9	9	10	-	-	-	
20	0	0	0	0	0	0	0	0	-	-	-	8	0	1	1	1	1	1	-	-	-	
21	1	1	1	0	0	0	0	0	-	-	-	12	0	1	2	2	1	1	-	-	-	