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Plasticity of life characteristics in two different populations of *Plantago maritima* L. (*)

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SUMMARY

A study was made of the nature of differences in life history characteristics of two neighbouring populations of *Plantago maritima* L. occurring in a salt marsh in the Netherlands.

A population of short-lived individuals whose reproduction was mainly generative was observed in high-lying, nearly ungrazed zones on sandy soil. A contrasting population of long-lived plants of *P. maritima* with a mainly vegetative reproduction was found in lower-lying grazed zones on a sandy clay soil.

The effects of the different soil types, differences in grazing intensity, inundation and salinity of both habitats on the percentage and rate of emergence, establishment, growth and reproduction of *P. maritima* were investigated.

It was shown that the life history characteristics of both populations were determined by the environmental factors occurring in both habitats.

It is postulated that the differences in life history characteristics between both populations were more likely to be due to phenotypic plasticity than to genetic variation.

KEY-WORDS: *Plantago maritima* - Phenotypic plasticity - Population ecology.

RÉSUMÉ

Une étude a été faite sur la nature des différences dans les cycles biologiques de deux populations voisines de *Plantago maritima* L. rencontrées dans une zone littorale salée des Pays-Bas.

Une population d'individus « à vie courte » dont la reproduction est essentiellement sexuée a été observée dans les zones élevées non pâturées sur sol sableux.

Une population différente de *P. maritima* « à vie longue » à reproduction essentiellement végétative se rencontre dans les parties basses pâturées, sur sol sablo-argileux.

On a étudié le rôle des différents types de sols, de l'intensité du pâturage, de l'inondation et de la salinité des deux habitats dans l'émergence, l'établissement, la croissance et la reproduction de *P. maritima*.

On a pu montrer que les cycles biologiques des deux populations sont déterminés par les facteurs écologiques caractérisant les deux habitats.

On en déduit que les différences entre les deux populations sont dues plutôt à une plasticité phénotypique qu'à des variations d'ordre génétique.

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INTRODUCTION

This study was initiated as part of a multidisciplinary project on the relationship between demographic, physiological and genetic properties of *Plantago* species and the characteristics of their environment. In this project the differences in life history between and within five *Plantago* species occurring in the Netherlands are being studied (VAN DER AART, 1979).

Changes in environmental circumstances may lead to changes in the life history characteristics of individual plants. In this respect, variation between individuals within one population is an important phenomenon. Two features can be distinguished. The first one is the genetic variability and the second the phenotypic plasticity, which results in a morphological plasticity based on variation in physiological processes (e. g. BRADSHAW, 1965; STEARNS, 1976; SOLBRIG *et al.*, 1979; ANTONOVICS & LEVIN, 1980). Differences in life history characteristics found between individuals from different populations of *P. lanceolata* L. can be generally ascribed to plasticity (WARWICK & BRIGGS, 1979; KUIPER & KUIPER, 1979), while in the case of *P. major* L. differences between individuals are mainly genetic (KUIPER, 1982). However, genetic differences between individuals of *P. lanceolata* within a population have also been found (VAN DAMME & VAN DELDEN, 1982). These differences refer to both nuclear and cytoplasmatic genes.

Intraspecific differences have been studied in many salt marsh plants. For example, SHARROCK (1967) showed that the differences in leaf forms of two populations of *Halimione portulacoides* (L.) Aellen are genetically determined. Intraspecific variation in *Suaeda maritima* (L.) Dum. was demonstrated by BOUCAUD (1962), in *Aster tripolium* L. by GRAY (1974), in *Limonium vulgare* Mill. by BOORMAN (1967), in *Salicornia europaea* L. and *Plantago maritima* by JEFFERIES (1977) and in *Puccinellia maritima* Huds. by GRAY & SCOTT (1980).

The main purpose of the present study was to investigate the nature of the relatively large differences in life characteristics between two neighbouring populations of *P. maritima* occurring at Kwade Hoek—a salt marsh on the island of Goeree (the Netherlands)—on two habitats which differed in soil type, tidal influences and grazing intensities. Preliminary studies on allozyme variation and morphological characteristics indicated that the differences between the two *P. maritima* populations probably had no genetic basis (VAN DIJK & VAN DELDEN, 1981 and H. VAN DIJK, personal communication). GREGOR (1938, 1939) and GREGOR & LANG (1950) described differences between populations of *P. maritima* from different areas. In Britain, these authors distinguished three ecotypes, occurring in distinct areas.

The present study tests the hypothesis that the differences in life history characteristics of the two neighbouring *P. maritima* populations are based on phenotypic plasticity. The environmental factors causing differences in life characteristics were studied. Field and laboratory experiments were performed to investigate the emergence of seeds landing in both habitats. Furthermore, the combined and separate effects of trampling, clipping and inundation on the establishment, growth and reproduction were investigated.

MATERIALS AND METHODS

The study area

The nature reserve Kwade Hoek (c. 315 ha) is situated on the island of Goeree in the southwest of the Netherlands. The vegetation of this tidal area ranges from halotypic communities on heavy

clay soils to communities growing on inland dunes with a sandy soil. The boundaries between the communities of some sites are quite distinct because of the presence of tidal creeks, whereas on the more interior sites the transition is more gradual as has also been described for other salt marshes by RANWELL, 1972; BEEFTINK, 1975, 1977; MAHALL & PARK, 1976. From May to October part of Kwade Hoek is grazed by cows. Phytosociological studies as well as species distribution in relation to edaphic factors were made by WESTHOFF *et al.*, 1961 and by BEEFTINK, 1975, 1977. Population I of *Plantago maritima* mainly occurs in the *Armerion maritimae* community. Other important taxa of this grazed community are *Glaux maritima* L., *Juncus gerardii* Loisl., *Festuca rubra* L., *Aster tripolium* L. and *Artemisia maritima* L. Population II of *P. maritima* occurs in low numbers at transitions between this community and the *Saginetum maritimae* community with *Sagina maritima* G. Don, *Plantago coronopus* L., *Cochlearia danica* L., *Honckenya peploides* (L.) Ehrh., *Centaurium littorale* (Turner) Gilmour, *Sagina nodosa* (L.) Fenzl. and *Festuca rubra* L. These transitions are found on a sandy soil with c. 4.4 mg Cl⁻ per 100 g dry soil, whereas the *Armerion maritimae* community is found on sandy clay soils containing c. 1,195 mg Cl⁻ per 100 g dry soil.

Population I occurs in lower zones with a layer of sandy clay in the upper soil with individuals with an estimated age of more than ten years. These plants propagate mainly vegetatively and only a few seedlings can be found. The mortality of these seedlings is very high. There is intensive grazing by cattle and regular flooding in these zones.

Population II is at the edge of the inner dunes. This zone is flooded only when the tide is extremely high and is seldomly grazed by cattle. In winter the grazing by rabbits is relatively high. In this upper zone with a sandy soil the individuals of *P. maritima* are short-lived. The estimated age is about three years. The reproduction of these plants in the field was observed to be mainly by seed which germinated rapidly, and established easily.

The distance between population I and population II is about 300 m. In 1970 a dam was built in a neighbouring estuary with the result that the high-water mark at Kwade Hoek increased. It is probable that since then population II of *P. maritima* has become established in the upper parts in the area.

Sowing experiments in the field

To get an impression of the germination and establishment of *P. maritima* in the field (Kwade Hoek), seeds were sown in four series of three plots (50 cm × 25 cm) each at the end of April 1980. These seedlings were observed for three successive years. Series *A* was situated in the direct surroundings of population II at the edge of the inner dunes, series *B* on a cattle path which was intensively trampled, series *C* near a creek at a site flooded during each high-tide period and series *D* on the site of population I, in a relatively dense vegetation layer. Series *A*, *B*, and *D* were flooded only during extremely high tides. On each plot 100 seeds, collected in the preceding year, were sown in a regular pattern at a depth of 0.5 cm. In the zones of series *A*, *B*, and *C* the naturally occurring numbers of *P. maritima* were relatively low (0-5 individuals per square metre). In series *D* c. 20 individuals per square metre were observed, and more rosettes per individual were sometimes found. The seedlings were mapped once a month, and after emergence of the plants the sowing patterns were generally clearly visible.

In August of three successive years the numbers of leaves, the length of the longest leaf, the propagation and mortality of the sown plants were recorded. In each zone the spontaneous emergence of *P. maritima* was observed at reference plots.

Since no significant differences in germination, seed weight, and cotyledon length were found between both populations, a mixed sample of seeds from both populations was used in all experiments.

Laboratory tests on the effects of soil type and salinity on germination

P. maritima seeds were placed on the sandy clay soil from the site of population I and on the sandy soils from the site of population II. Two layers of both soil types were tested: 0.2 cm and 3-10 cm, respectively. This experimental lay-out was chosen because in the field, soil is often disturbed by animals, which may result in the seeds being moved vertically in the soil.

The seeds used were stored at 5° C for 2 years; triplicate tests with 50 seeds each were performed

in the greenhouse (18° C, photoperiod 18 hours). The moisture content of the clay and sandy soils was maintained at 30 % and 18 % by weight, respectively.

In this experiment a reference test on filter paper was added. In a separate experiment sandy soils were moistened with the following concentrations of seawater: 100 % (1.78 % Cl⁻), 50 %, 25 %, 12.5 % and 0 %, respectively. The moisture content of the substrate was maintained at 18 % by weight.

Grazing simulation experiments in the laboratory

a) *Pot experiments with single plants.*

In order to investigate two effects of grazing on development and reproduction of *P. maritima*, clipping and trampling separately and in combination were studied. The following treatments were applied to individual plants.

- Weekly clipping at a height of 5 cm above the soil surface.
- A trampling treatment for 5 seconds with a pressure of 0.25 kg/cm² once a day. LIDDLE (1975) found similar values for the vertical forces applied to the ground by man.
- Weekly clipping combined with daily trampling.
- Control plants, no treatment.

The treatments started six weeks after sowing. All series consisted of 20 plants, grown separately in one-litre pots filled with a sandy substrate. Nutrient conditions were optimal. Light intensity at plant level was about 33 W/cm². Each week, the length of the longest leaf, the number of leaves, the number of flowering plants, the number of spikes, and the number of daughter rosettes were determined.

b) *Pot experiments with turves.*

In a separate experiment the effects of trampling on *P. maritima* seedlings growing in the vegetation were investigated. For this aim, turves of 20 cm × 20 cm × 25 cm (thickness) from the site of population I (cattle-grazed area of Kwade Hoek) were collected and placed in pots in the greenhouse (soil moisture 25 % by weight). Fifty seedlings a week old were planted in the turves. After 10 days the number of seedlings was reduced to 25 individuals per pot in such a way that the remaining seedlings were distributed uniformly over the turf. A trampling treatment, comparable with that of the former experiment (single plants in pots) was applied. A reference series without trampling was added. The tests were carried out in duplicate; once a fortnight the surrounding vegetation in the turves was clipped to the same height as the *Plantago* plants. Each week, the numbers of dead seedlings, the length of the longest leaf per plant, the numbers of leaves per plant and the number of flowering plants were determined.

Simulation of inundation

To study the effects of regular flooding with sea water, the following experiment was carried out in the greenhouse. The various treatments started six weeks after germination.

- Every other day soils with *P. maritima* were saturated with sea water by capillary rise for four hours. On the intermediate days the soils were watered with fresh water to prevent the accumulation of salt in the upper soil layers. Once every fortnight sea water was poured over the soil, until the soil was saturated. This treatment was carried out to simulate high tide.
- In a control series fresh water was used instead of sea water.

Both series consisted of 20 plants, grown separately in one-litre pots filled with a sandy substrate. Nutrient conditions were optimal.

In this test the light intensity at plant level was 28 W/m². The sea water originated from the North-sea at the Kwade Hoek.

Plant characteristics were determined in the same way as in the grazing simulation tests.

RESULTS

Sowing experiments in the field

Table I shows the species composition of the *P. maritima* sowing plots at Kwade Hoek. The percentages emerged and dead seedlings of *P. maritima* in the first year

TABLE I. — Description of the vegetation of sowing plots at Kwade Hoek.
Per species the percentages of cover are given. The descriptions were made in August of 1980.

	Edge of inner dunes A	Cattle path B	Edge of creek C	Cattle- grazed dense vegetation D
<i>Plantago maritima</i>	5-10	< 5	—	10-15
<i>Plantago coronopus</i>	5-10	—	—	< 5
<i>Carex arenaria</i>	5-10	—	—	—
<i>Honckenya peploides</i>	10-15	< 5	—	—
<i>Festuca rubra</i>	< 5	—	—	25-30
<i>Atriplex hastata</i>	5-10	—	—	< 5
<i>Spergularia media</i>	< 5	5-10	< 5	—
<i>Poa pratensis</i>	10-15	< 5	—	—
<i>Juncus gerardii</i>	—	—	< 5	65-70
<i>Salicornia europaea</i>	—	< 5	—	—
<i>Puccinellia maritima</i>	—	—	35-40	—
<i>Glaux maritima</i>	—	—	40-45	25-30
<i>Aster tripolium</i>	—	—	—	< 5
Total cover	60	20	80	100
Maximum height of herb layer....	5-15 cm	5 cm	5 cm	5 cm
— not present				

are given in figure 1. In all plots the first seedlings were visible three weeks after sowing. In the highest-lying zone (series A) germination occurred throughout the season. At the end of the season no significant differences in emerged and dead seedlings were observed between the plots of series A. On the cattle path (series B) the total emergence of *P. maritima* was about 10 % in each of the three plots. A small wave of secondary emergence in plots B_{II} and B_{III} was observed in August (fig. 1). At the end of the season all plants from sown seeds were dead. On the regularly flooded plots (series C, fig. 1), emergence occurred soon after sowing. The total emergence of *P. maritima* in plot C_{III} was significantly lower ($P < 0.05$) than that in plots C_I and C_{II}. In the first months after sowing, the mortality of *P. maritima* in the plots along the creek was lower than that of the plants sown on the cattle path (series B). However, along the creek (series C) nearly all the seedlings died off in August. Due to the daily flooding, the soil of series C was very marshy. The roots of many seedlings were evidently knocked loose frequently. Trampling by cows reinforced this phenomenon. In the dense vegetation layer of series D up to 20 % of the sown seeds emerged as seedlings. During the season the mortality of the plants in the plots D_{II} and D_{III} was relatively low (fig. 1). In these grassy plots the plants were able to maintain themselves relatively well. More flowering plants were found in the high-lying zones whereas *P. maritima* reproduced mainly vegetatively in the dense vegetation layer of series D (table II). At this site the mortality was significantly lower than in the high-lying zone. The emergence of seedlings in the reference plots was very low. A maximum of 4 naturally occurring seedlings was observed in the reference plots.

Laboratory tests on the effects of soil type and salinity on germination

Figure 2 shows the emergence of *P. maritima* on sandy clay and sandy soils from populations I and II, respectively. No germination was found in the upper sandy

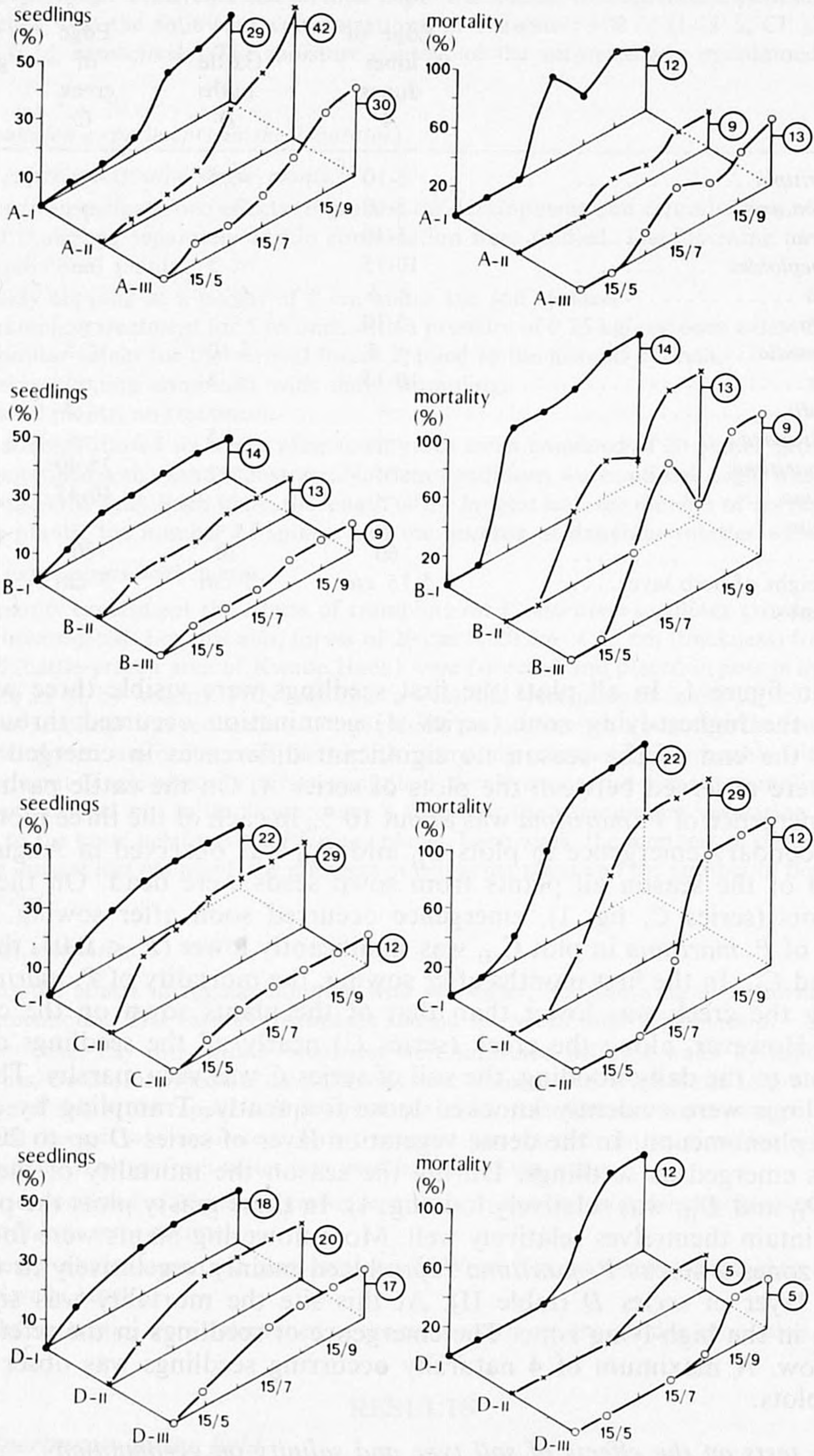


FIG. 1.

TABLE II. — Some demographic characteristics of *Plantago maritima* measured in August of three successive years. In 1980 seeds were sown on plots at the edge of the inner dunes (series A, site of population II) and on plots on cattle-grazed zones (series D, site of population I) in the salt marsh Kwade Hoek (the Netherlands).

	1980		1981				
	Mean number of leaves per plant	Mean length of longest leaf (mm)	Mean number of leaves per plant	Mean length of longest leaf (mm)	% flowering plants	% plants with rosettes	Mortality (%)
<i>A_I</i>	5.0 ± 0.4	19.1 ± 4.1	8.2 ± 1.3	68.1 ± 3.1	66.7	0	47.1
<i>A_{II}</i>	4.6 ± 0.3	15.2 ± 1.4	6.9 ± 0.8	72.3 ± 5.4	55.6	0	41.9
<i>A_{III}</i>	5.2 ± 2.3	11.7 ± 1.9	8.1 ± 3.5	65.7 ± 2.9	60.0	0	70.6
<i>D_I</i>	2.8 ± 0.3	48.5 ± 8.4	5.4 ± 0.4	40.4 ± 2.7	0	40.0	16.7
<i>D_{II}</i>	1.9 ± 0.2	21.4 ± 1.4	5.2 ± 0.3	61.5 ± 2.9	0	25.0	13.3
<i>D_{III}</i>	2.1 ± 0.2	16.7 ± 0.9	5.2 ± 0.4	51.3 ± 2.6	0	12.5	33.3

	1982				
	Mean number of leaves per plant	Mean length of longest leaf (mm)	% flowering plants	% plants with rosettes	Mortality (%)
<i>A_I</i>	7.1 ± 1.4	70.1 ± 4.2	75.0	0	55.6
<i>A_{II}</i>	5.8 ± 1.1	67.7 ± 2.8	83.3	16.7	66.7
<i>A_{III}</i>	6.7 ± 0.9	63.9 ± 3.3	50.0	0	60.0
<i>D_I</i>	5.4 ± 0.5	38.8 ± 2.7	0	75.0	20.0
<i>D_{II}</i>	2.4 ± 0.2	21.6 ± 2.9	22.2	66.7	25.0
<i>D_{III}</i>	4.5 ± 0.3	31.3 ± 2.7	16.7	5.0	37.5

FIG. 1. — Series A. Germination and mortality of *Plantago maritima* sown on the edge of the inner dunes at Kwade Hoek (Goeree, the Netherlands). The percentages of emerged plants are given in relation to the numbers of seeds sown. The percentages of dead individuals were calculated with reference to the numbers of seedlings which emerged in the preceding period.

Series B. Germination and mortality of *Plantago maritima* sown on a cattle path.

Series C. Germination and mortality of *Plantago maritima* sown near a creek, flooded during each high-tide period.

Series D. Germination and mortality of *Plantago maritima* sown near a creek, flooded only during extremely high tides.

(22) Number of emerged or dead seedlings.

clay layers of 0-2 cm. The salinity in the upper sandy clay layer was high (1,195 mg Cl^- per 100 g dry soil) and in the lower sandy clay layers relatively low (490 mg Cl^- per 100 g dry soil). It should be noted that in the sandy soil no differences in germination behaviour were found between the upper and lower layer. The salinity in both of these layers was very low (4.4 mg Cl^- per 100 g dry soil). Furthermore, the stepwise germination in the sandy soil was not observed in the lower sandy clay soil.

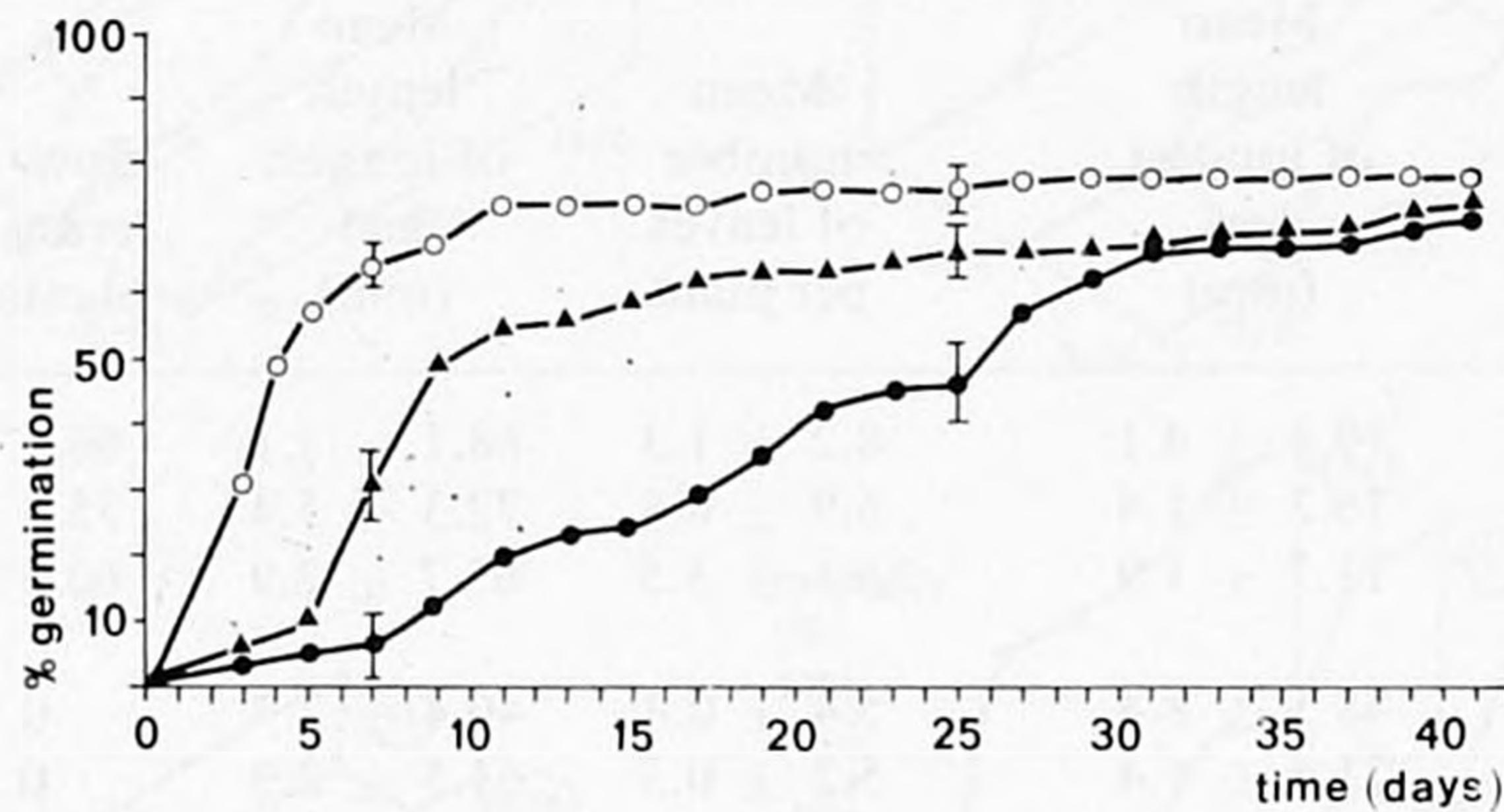


FIG. 2. — The germination of *Plantago maritima* on sandy clay soils and on sandy soils.

- sandy soil (from 0-2 cm depth),
- ▲—▲ sandy clay soil (from 3-10 cm depth),
- controls in Petri dishes on filter paper with distilled water,

I 2 S. E.

It is obvious that the germination rate during the first period of the test was considerably lower on the sandy soil than on the sandy clay soil. At the end of the test no significant differences in the total numbers of germinated seeds were observed between sandy soil and the lower sandy clay soil. Table III shows the percentages of emerged *P. maritima* seedlings on sandy soils at different Cl^- concentrations. Percentages of 25 % sea water and more caused a significant decrease in emergence.

TABLE III. — Final percentages of the emerged *Plantago maritima* seedlings after 21 days on sandy soils with different salinity levels.

Salinity as percentage of sea water (1.78 % Cl^-)	Emerged seedlings (mean percentage \pm S. E.)
100	0
50	7.6 \pm 5.2
25	66.0 \pm 4.6
12.5	78.0 \pm 2.6
6.25	89.0 \pm 1.0
0	86.7 \pm 2.8

Grazing-simulation experiments in the laboratory

a) Pot experiments with single plants.

In order to estimate the biomass of the upper parts of the *P. maritima* plants, the number of leaves per plant as well as the length of the longest leaf was measured

(fig. 3 a, b). Former experiments with *Plantago* species showed that the multiplication of these values gives an estimate of the biomass (NOË & BLOM, 1982). At the end of the test the approximated biomass of trampled plants was significantly higher ($P < 0.05$) than that of the control series (fig. 4 a). This was caused mainly by a significant increase in the numbers of leaves per plant in the trampled series (fig. 3 a). The length of the longest leaves of trampled plants being significantly less than that of plants in the control series (fig. 3 b). This phenomenon was also found for trampled *P. major* plants (VAN HEESWIJK & BLOM, 1981). In the series in which the leaves were cut, no increase in the numbers of leaves per plant was found (fig. 3 a).

In the trampled series and in the control about 95 % of the plants had formed daughter rosettes at the end of the experiment. Compared with the control plants the mean number of rosettes per individual was significantly higher in the trampled series (fig. 4 b).

In contrast, the number of flowering plants was significantly higher in the controls (85 %) than in the trampled group (64 %), whereas the mean number of spikes per plant was significantly the highest in the trampled series (11.4 spikes per plant compared to 8.6 in the controls). In none of the other treatments (clipping and trampling combined with clipping) did the plants flower or reproduce vegetatively.

b) *Pot experiments with turves.*

A vegetation analysis of the turves is given in table IV. Due to the trampling treatments, in the turves relatively many seedlings died off in the first weeks of the experiments (in the duplicate tests: 59 % and 66 %, respectively; 0 % in the controls).

TABLE IV. — Description of the vegetation of turves collected from the cattle-grazed area at the salt marsh Kwade Hoek. The percentages of soil coverage of the species are given before the planting of *Plantago maritima* seedlings and after the planting and trampling treatment at the end of the test (14 weeks). Since only small differences between the duplicate series occurred, one description is given from each of the controls as well as of the trampled series.

	Control series		Trampled series	
	before planting	after planting	before planting	after planting
<i>Juncus gerardii</i>	35-45	35-45	35-45	15-25
<i>Glaux maritima</i>	25-35	35-45	25-35	5-15
<i>Agrostis stolonifera</i>	25-35	55-65	15-25	25-35
<i>Festuca rubra</i>	45-55	35-45	35-45	5-15
<i>Plantago maritima</i>	5-15	15-25	5-15	< 5
<i>Plantago coronopus</i>	< 5	5-15	—	—
<i>Carex distans</i>	—	< 5	—	—
<i>Centaureum pulchellum</i>	< 5	< 5	< 5	—
<i>Aster tripolium</i>	< 5	—	—	—
<i>Trifolium fragiferum</i>	—	—	< 5	—
— not present				

In order to get an impression of the course of the biomass production, the numbers of leaves as well as the length of the longest leaf per plant were determined during the experiment (fig. 5 a, b). In the controls the approximated biomass production of the *P. maritima* plants was significantly higher than in the trampled turves (fig. 6), which

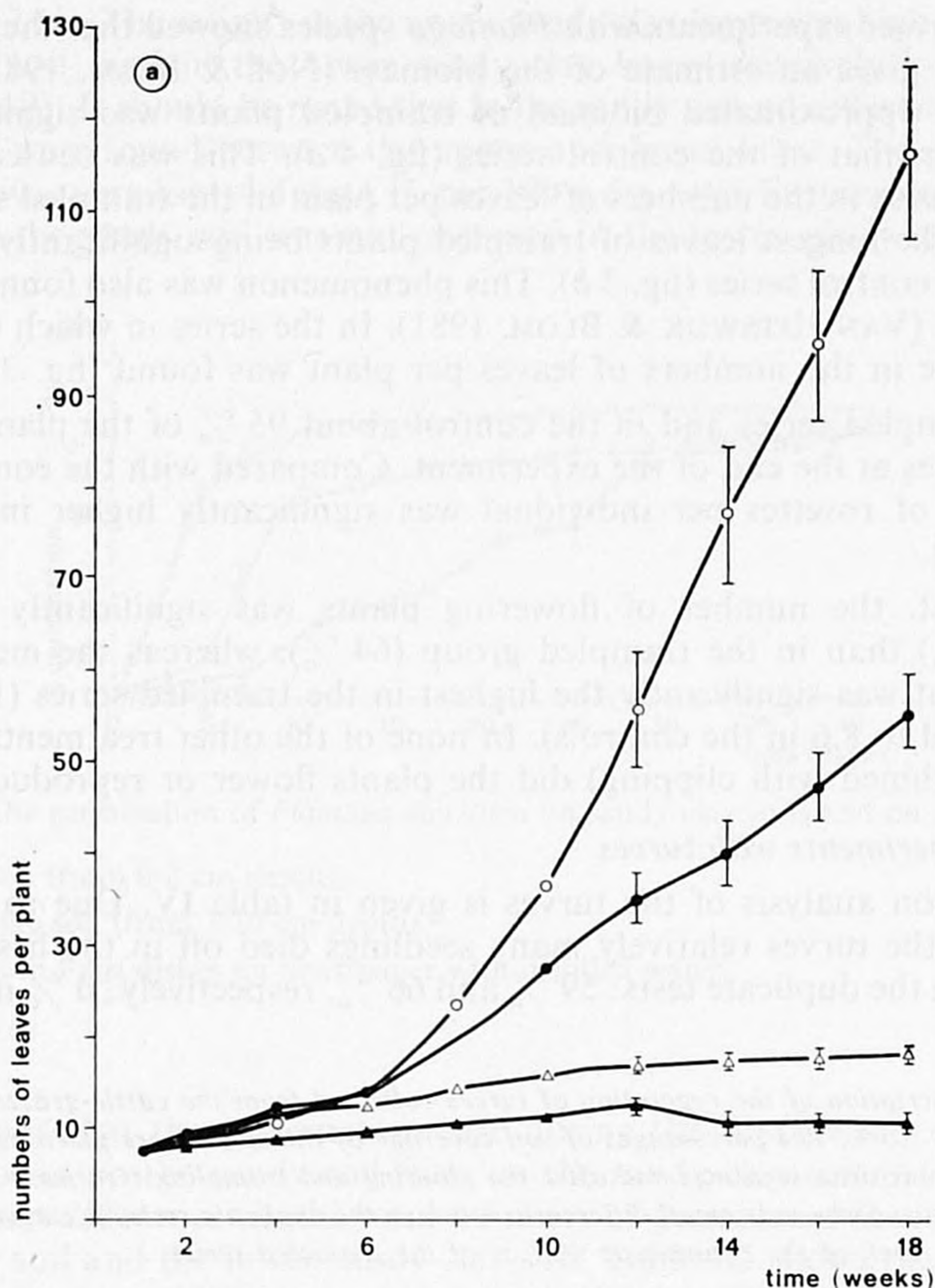


FIG. 3 *a, b*. — The effects of clipping and trampling on the mean numbers of leaves per plant (*a*) and the mean length of the longest leaf (*b*) of *Plantago maritima* plants grown separately in pots in the greenhouse.

- Δ — Δ clipping treatment,
- — ○ trampling treatment,
- ▲ — ▲ combined trampling and clipping,
- — ● controls,

I 2 S. E.

was caused mainly by the fact that the leaves of the trampled plants were relatively small (fig. 5 *b*). The number of leaves remained behind that of the control plants (fig. 5 *a*). In this experiment only in the control series flowering *P. maritima* plants were observed. Flowering started after about 7 weeks and at the end of the test less than 10 % of the plants flowered, each plant with only a few spikes. In both series no daughter rosettes were found.

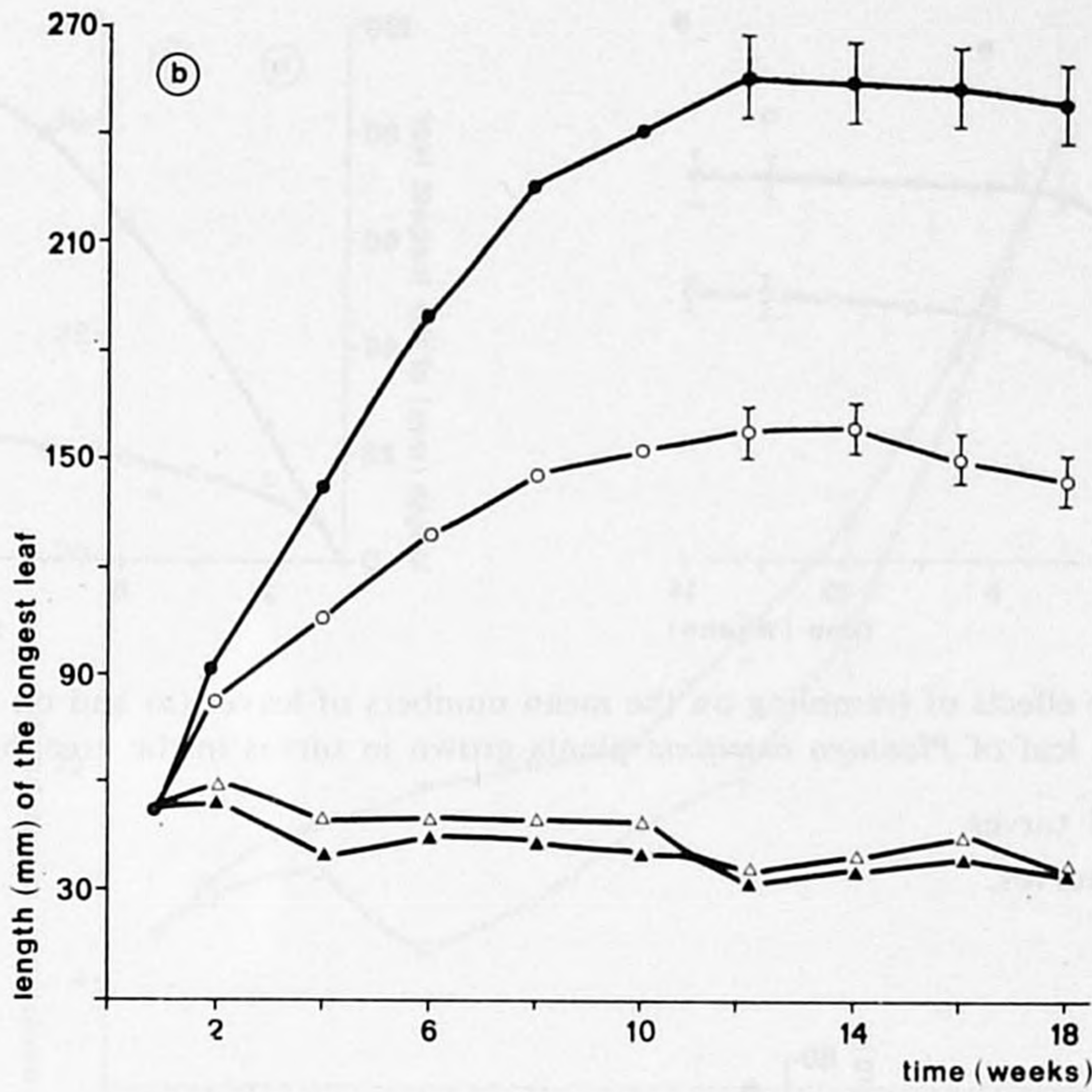


FIG. 3 *a, b* (continued).

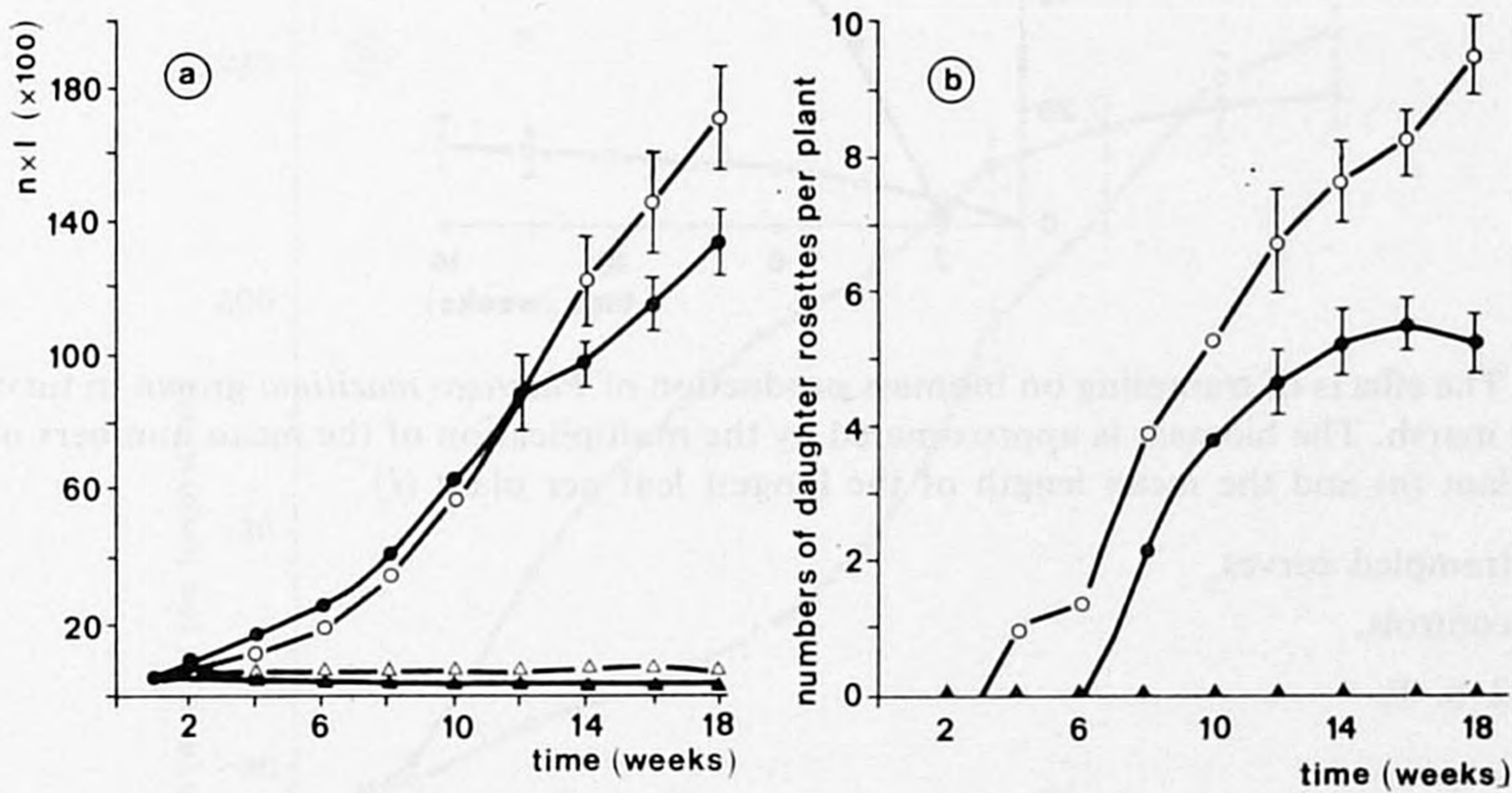


FIG. 4 *a, b*. — The effects of clipping and trampling on biomass production (*a*) and on the mean numbers of daughter rosettes per plant (*b*) of *Plantago maritima* grown separately in pots in the greenhouse. The biomass is approximated by the multiplication of the mean numbers of leaves per plant (*n*) and the length of the longest leaf per plant (*l*).

- Δ — Δ clipping treatment,
- — ○ trampling treatment,
- ▲ — ▲ combined clipping and trampling,
- — ● controls,

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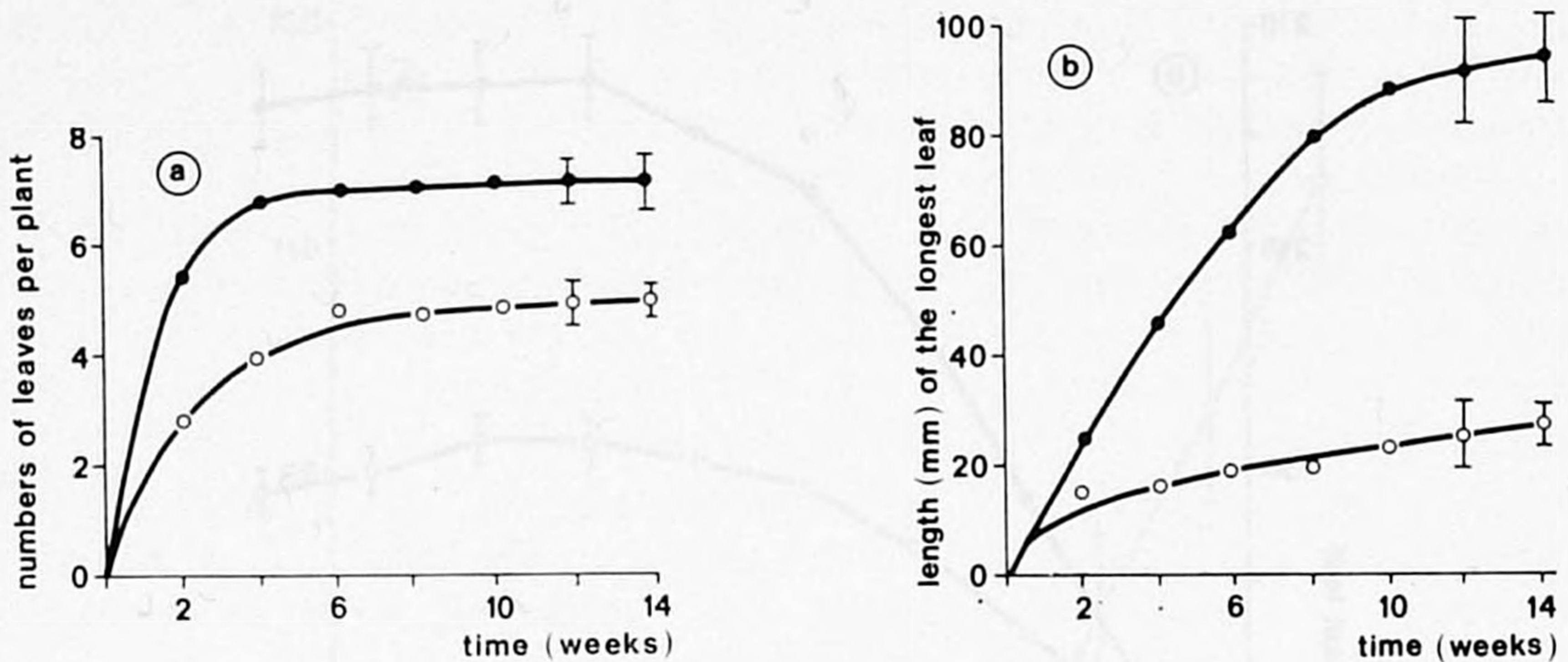


FIG. 5 *a, b*. — The effects of trampling on the mean numbers of leaves (*a*) and on the mean length of the longest leaf of *Plantago maritima* plants grown in turves in the greenhouse.

- — ○ trampled turves,
 ● — ● control turves,
 I 2 S. E.

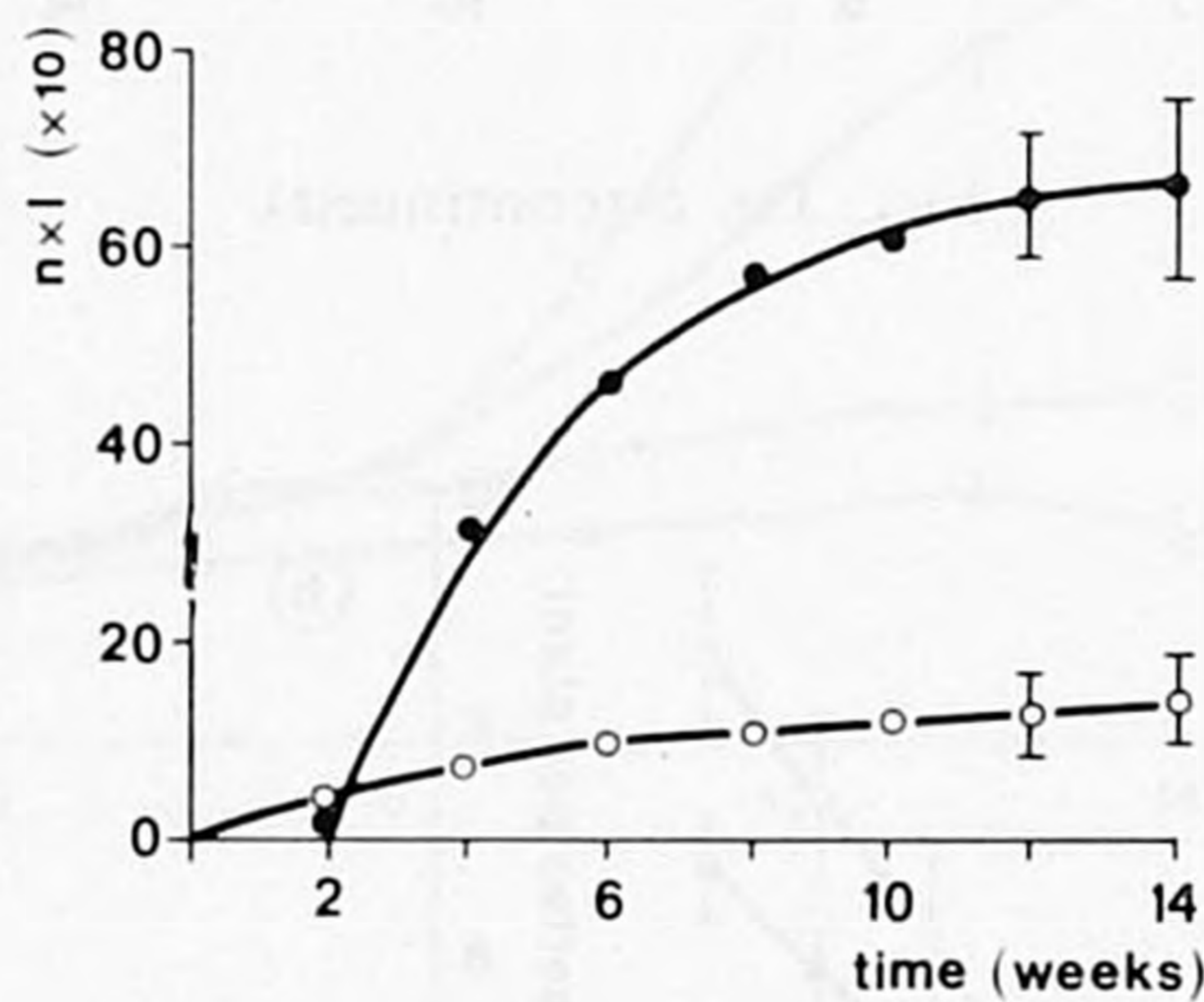


FIG. 6. — The effects of trampling on biomass production of *Plantago maritima* grown in turves from a salt marsh. The biomass is approximated by the multiplication of the mean numbers of leaves per plant (n) and the mean length of the longest leaf per plant (l).

- — ○ trampled turves,
 ● — ● controls,
 I 2 S. E.

Simulation of inundation in the laboratory

Figure 7 *a, b* shows the numbers of leaves as well as the length of the longest leaf per inundated *P. maritima* plant. Figure 8 *a* shows the approximated biomass production during the experiment. At the end of the experiment no significant differences were found between the approximated biomass of the sea water plants and that of the plants inundated with fresh water (controls). However, the rate of biomass production during the first seven weeks was higher in the control series. In the first period of this experiment the increase in biomass of the fresh water plants could be especially ascribed to the increase in the length of the leaves (fig. 7 *b*), whereas in the

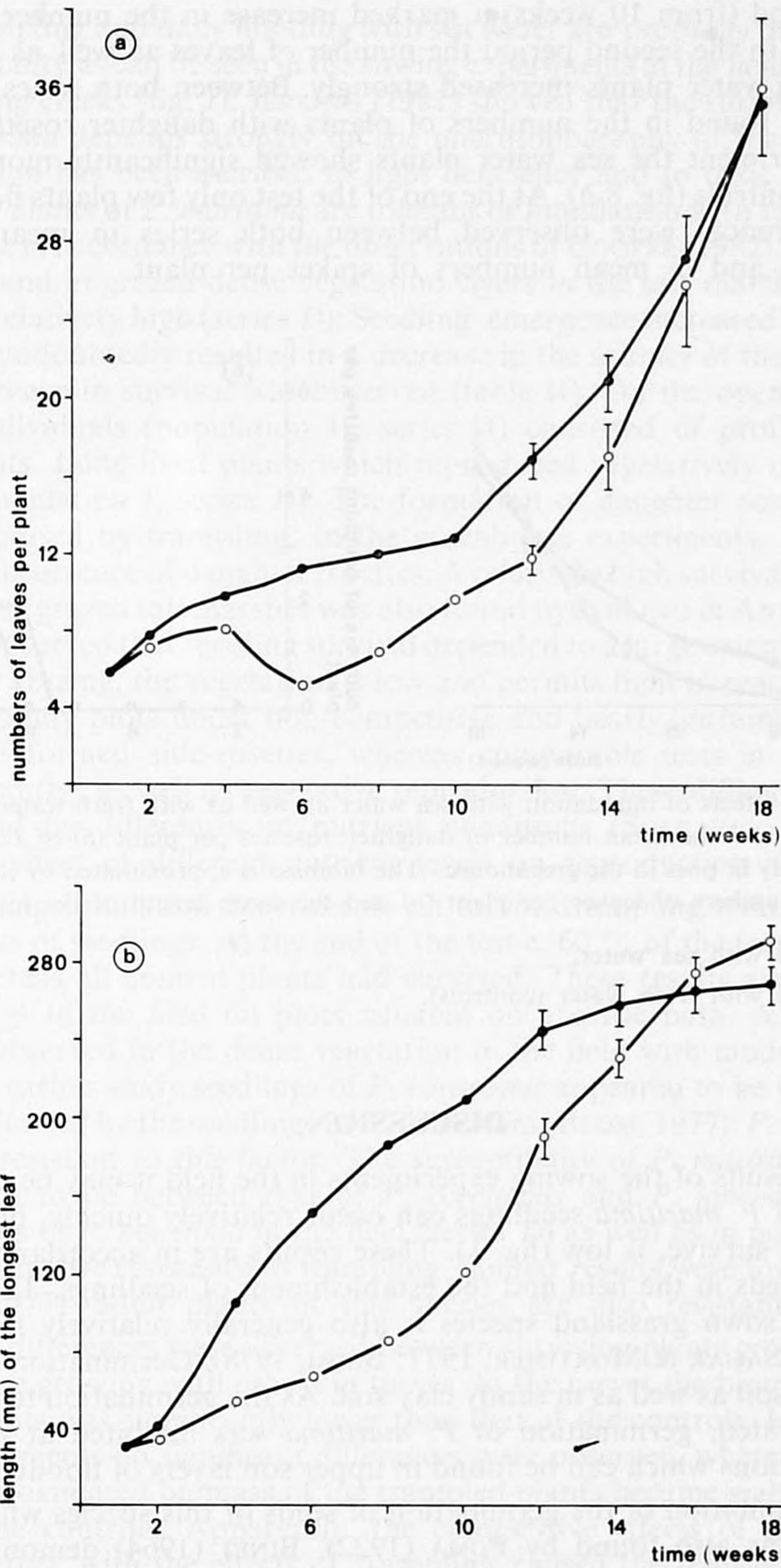


FIG. 7 *a, b*. — The effects of inundation with sea water as well as with fresh water on the mean numbers of leaves per plant (*a*) and on the mean length of the longest leaf (*b*) of *Plantago maritima* plants grown separately in pots in the greenhouse.

○ — ○ inundated with sea water,
 ● — ● inundated with fresh water (controls),
 I 2 S. E.

subsequent period (from 10 weeks) a marked increase in the number of leaves was found (fig. 7 *a*). In the second period the number of leaves as well as the size of the leaves of the sea water plants increased strongly. Between both series no significant differences were found in the numbers of plants with daughter rosettes, but at the end of the experiment the sea water plants showed significantly more rosettes per plant than the controls (fig. 8 *b*). At the end of the test only few plants flowered and no significant differences were observed between both series in mean numbers of flowering plants and in mean numbers of spikes per plant.

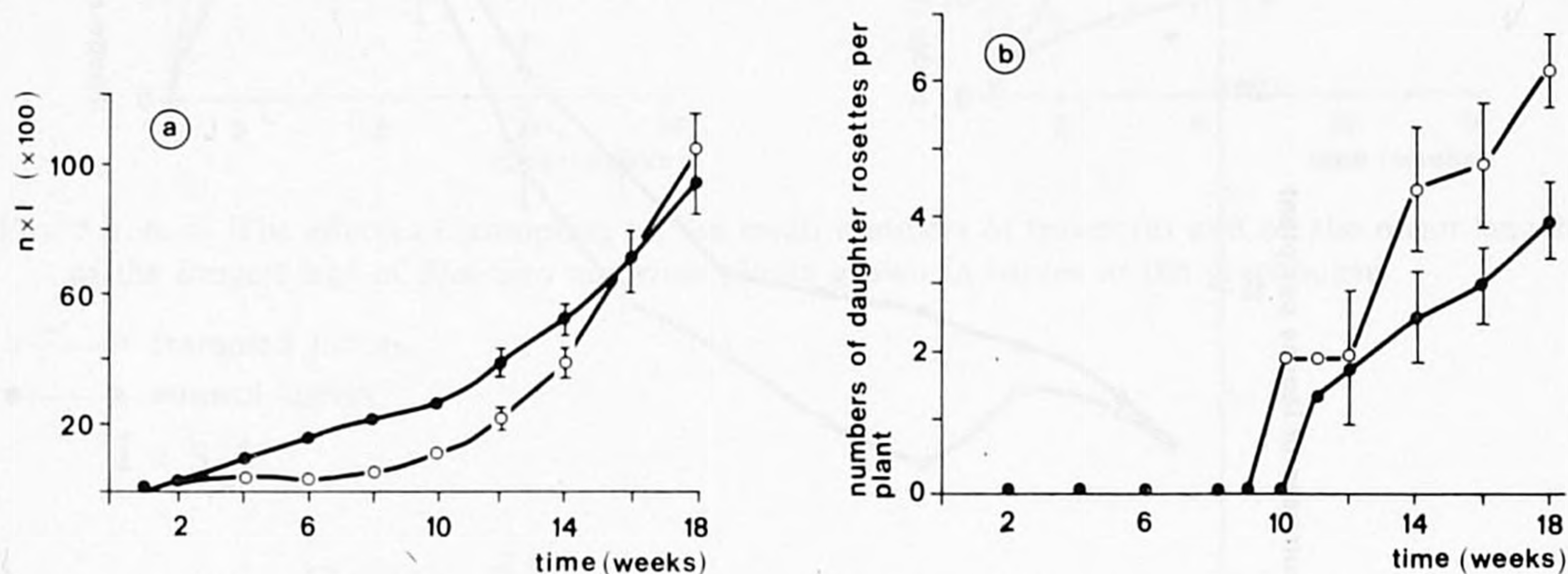


FIG. 8 *a, b*. — The effects of inundation with sea water as well as with fresh water on the biomass production (*a*) and the mean number of daughter rosettes per plant (*b*) of *Plantago maritima* grown separately in pots in the greenhouse. The biomass is approximated by the multiplication of the mean numbers of leaves per plant (n) and the mean length of the longest leaf (l).

- — ○ inundated with sea water,
 ● — ● inundated with fresh water (controls),
 I 2 S. E.

DISCUSSION

From the results of the sowing experiments in the field it may be concluded that the emergence of *P. maritima* seedlings can occur relatively quickly, but the number of seedlings that survive, is low (fig. 1). These results are in accordance with studies on the fate of seeds in the field and the establishment of seedlings. The germination and survival of sown grassland species is also generally relatively low under field conditions (*e. g.* SAGAR & MORTIMER, 1977; BLOM, 1978). Germination of *P. maritima* occurs in sandy soil as well as in sandy clay soil. As the germination tests in the laboratory demonstrated, germination of *P. maritima* was inhibited at relatively high NaCl-concentrations which can be found in upper soil layers of flooded salt marshes.

Increased inhibition of the germination of seeds of this species when the salinity was increased was also found by POMA (1922). BINET (1964) demonstrated that a pretreatment with salt water caused an increased germination of fresh seeds, which was also found with, for example, *Glaux maritima* by ROZEMA (1975). Many authors have reported that the highest germination of halophytes occurs most frequently under freshwater conditions (*e. g.* ROZEMA, 1975; FREIJSEN, 1971; TREMBLIN & BINET, 1982); the germination capacity of only a few species seems to improve under sea water conditions (*e. g.* UNGAR, 1962; MAYER & POLJAKOFF-MAYBER, 1982; BOORMAN, 1968).

Heavy trampling and daily flooding with sea water are probably important causes of seedling mortality as can be seen in the sowing experiments in the field on cattle paths and at sites along creeks (fig. 1). JERLING (1981) showed that the survival of the seedlings of *P. maritima* depends strongly on the microtopography of the soil. Mortality due to inundation has been ascribed to light deficiency and to toxic effects of H_2S . However, adult plants of *P. maritima* are tolerant of inundation with sea water (fig. 8). These results are in accordance with the observations of COOPER (1982). On open sandy soils (series A) and in grazed dense vegetation layers in the salt marsh, seedling establishment was relatively high (series D). Seedling emergence increased after periods of rainfall, which undoubtedly resulted in a decrease in the salinity of the soil. However, a marked difference in survival was observed (table II). On the open sandy soil the *P. maritima* individuals (population II, series A) consisted of profusely flowering short-lived plants. Long-lived plants which reproduced vegetatively occurred on the grazed sites (population I, series D). The formation of daughter rosettes (series D) was probably caused by trampling: in the greenhouse experiments, trampling, too, resulted in the occurrence of daughter rosettes. A relatively high survival of *P. maritima* seedlings in dense grazed salt marshes was also found by JERLING & ANDERSSON (1982). These authors observed that seedling survival depended to a large extent on the amount of light. Due to grazing, the vegetation is low and permits light to reach the seedlings. In the field at sandy plots under non-competitive and nearly untrampled conditions, only few plants formed side-rosettes, whereas comparable tests in the greenhouse resulted in generative as well as vegetative reproduction. These different reactions are probably caused by differences in nutrient conditions (SOEKARJO, 1981). Further studies on the effect of different nutrient levels on reproduction are in progress.

In the grazing-simulation experiments on turves, trampling treatments caused a considerable loss of seedlings. At the end of the test c. 60 % of the trampled seedlings were dead, whereas all control plants had survived. These results are in accordance with the findings in the field on plots situated on a cattle path. A lower seedling mortality was observed in the dense vegetation in the field with moderate trampling by cattle. In an earlier study seedlings of *P. coronopus* appeared to be very susceptible to trampling followed by the seedlings of *P. lanceolata* (BLOM, 1977). *P. major* seedlings were the most resistant to this factor. The susceptibility of *P. maritima* seedlings to trampling seems to be between that of *P. coronopus* and *P. lanceolata*. However, full-grown plants of *P. maritima* in the field (series D) as well as in pots in the greenhouse showed a higher resistance to trampling. Similar results were found for *P. coronopus* (BLOM, 1977); adult plants of this species are also resistant to trampling.

Interesting differences were observed between surviving plants growing separately in pots and those growing with others in turves. In the turves the biomass production of trampled plants was significantly lower than that of the controls. In the first stage of the pot experiments no significant differences were observed, whereas at the end of the test the approximated biomass of the trampled plants became significantly higher than that of the controls. Apparently, the competitive effects of the surrounding vegetation together with the effects of trampling caused the reduced growth of the trampled *Plantago* plants in the turves. In the field experiments, a reduced biomass production of *P. maritima* was also found in the zones with the dense vegetation layer (table II). The results of these series of experiments prove again that a direct translation of results obtained in tests carried out in the greenhouse with plants growing separately in pots to the real situations in the field is very dangerous. Experiments performed with turves can be a valuable link between both situations, and may help to give a correct interpretation of the behaviour of plants in the field.

Furthermore, these series of experiments proved that the differences in life characteristics between individuals of the two populations of *P. maritima* at the salt marsh Kwade Hoek are mainly based on different biotic and abiotic factors. In all experiments seeds from the same seedpool were used. Trampling and inundation, combined with the presence or absence of surrounding plants resulted in individuals differing in such characteristics as emergence, seedling establishment, adult survival, growth and form of reproduction. It is likely that under field conditions, in a regularly flooded salt marsh, with the activities of wild and domestic grazing animals, seeds of *P. maritima* from different sites will be dispersed over large surfaces which leads to mixtures of seeds from the different zones (cf. JERLING, 1982). Nevertheless marked differences in demographic characteristics between populations are observed in the field. The experiments described in this paper indicate that these striking differences are, to a large extent, based on phenotypic plasticity.

GREGOR & LANG (1950) postulated that the European sea plantain is highly variable and that few local populations entirely lack genetic individuality. The present study suggests that local differences between life history characteristics of two neighbouring populations of *P. maritima* are probably caused by phenotypic physiological adaptation on different environmental conditions. In spite of the contrasting types of selection, no indication of genetic differences between both populations exists at the moment. This phenomenon is probably caused on the one hand by the small distance between both populations in the field and on the other by the fact that the establishment of population II occurred only about ten years ago. However, it is possible that in the long-term selection between the grazed and the scarcely grazed populations of *P. maritima* may lead to genetic differentiation (cf. JEFFERIES, 1977).

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