Journal of Coastal Research	3	3	359-368	Charlottesville	Summer 1987

Comparative Ecophysiological Studies on *Puccinellia maritima* and *Festuca rubra*, Bank End Coastal Marsh, Irish Sea, England[1]

M.A. Zahran

Botany Department
Faculty of Science
Mansoura University
Mansoura, Egypt

ABSTRACT

ZAHRAN, M.A., 1987. Comparative ecophysiological studies on *Puccinellia maritima* and *Festuca rubra*, Bank End coastal marsh, Irish Sea, England. *Journal of Coastal Research*, 3(3), 359-368. Charlottesville, ISSN 0749-0208.

This paper deals with an ecophysiological study of two salt marsh grasses: *Puccinellia maritima* and *Festuca rubra*. They dominate the second and third zones of Bank End marsh on the Irish Sea, northwest of England. Three types of experiments (germination, glasshouse and field) were conducted to shed light on their zonation patterns, response to mineral nutrients and tolerance to salinity. The results of these experiments indicate that a combination of several factors (tidal movements, relief, soil salinity etc.) controls the zonation of the two communities but their individual effects differ. Tidal movement and ground relief are major environmental factors. Because both species are salt-tolerant and the salinities of their soils are almost comparable, salinity seems to play a less important role. Nitrogen deficiency is harmful to the growth of both species The absence of phosphorus causes a slight decrease in yields.

ADDITIONAL INDEX WORDS: *Irish Sea*, Puccinellia maritima, Festuca rubra, *Bank End marsh, salinity, tidal movement, ground relief.*

INTRODUCTION

The present work deals with an ecophysiological study on two salt marsh grasses, *Puccinellia maritima* (Huds.) Parl. (sea poa) and *Festuca rubra* L. (creeping fescue). Both are common grasses in marshes and muddy estuaries of Britain and continental Europe. They are also recorded in North America and northern Africa (CLAPHAM *et al.*, 1962; BUTCHER, 1961). The aim of this work was to study the growth of *Puccinellia* and *Festuca* in salt marsh habitats with particular reference to factors that might control their zonation in littoral marshes. Bank End marsh was assumed to be a typical example.

ECOLOGICAL CHARACTERISTICS OF BANK END MARSH

Bank End marsh is located on the Irish Sea about 35 km west of Lancaster (northwest England) where the general climate is cool. The lowest means of temperature (4.5° C, 3.4° C and 3.6° C) and the shortest periods of sunshine hours per day (1.2, 1.6 and 2.4) are recorded during the winter months, *i.e.* December, January and February, respectively. By contrast, the summer months have the highest means of temperature and the longest hours of sunshine per day (14° C and 6.7 hrs in June, 15.5° C and 5.2 hrs in July and 15.4° C and 5 hrs in August). Rainfall (100.5 ml) is distributed over the whole year, the highest monthly rainfall (11.25 ml) occurring in April. Evaporation is 40.0 ml per year. In May, evaporation (7.24 ml) slightly exceeds the rainfall. This can be expected in June. In July and August, rainfall exceeds evaporation in both months by about 3.75 ml. The average wind velocity over the ridge is often high.

Bank End marsh is charactcrized by three vegetation zones: (1) The first zone is occupied by a *Salicornia europaea* community which forms an almost pure growth. It is flooded with seawater at all times except during a few hours at neap tide. The soil is composed of clay and silt and is usually wet and slippery. Its pore spaces range between 43.2%

[1]*This work was supported by a British Council fellowship at the Biology Department, University of Lancaster, England. 84040 received 20 December, 1984; accepted in revision 14 June 1985.*

water as required. The experiment lasted ten weeks and then the plants were harvested.

The results of this experiment, displayed in Table 2a, show that (1) the total yields of *Puccinellia* plants were higher (more than five times that of *Festuca* plants), (2) the leaf length of both species was longer in soil culture and that (3) high concentrations of seawater (1:10, 1:2 and 1:00) retarded the growth of both species in the two cultures.

(b) Seedlings germinated in the lab. In this trial *P. maritima*, *F. rubra* (marsh) and *F. rubra* (inland variety S59) seeds were germinated. The same dilutions of seawater were applied to six groups of small pots (twelve pots for each group). Sixteen seedlings of *P. maritima* were transplanted in four pots of each group. The same was repeated for the two varieties of *F. rubra*. The experiment lasted for seven weeks. The plants were watered with distilled water when necessary and then harvested. Their oven-dry weights were determined in the usual manner. The results (Table 2b) indicate that a successive increase in yield, expressed by the mean oven-dry weights of *Puccinellia* plants, was obtained as the concentration of seawater increased from 2.93 mg at 1:100 to 11.89 mg at 1:00 or 100% seawater. A comparable increase was observed in the *Festuca* marsh plants up to 1:2 dilution (from 7.58 mg to 12.02 mg). At 100% seawater treatment, the dry weight of *Festuca* dropped to 4.92 mg. On the other hand, the optimal dilution of seawater favoring the growth of inland *Festuca* (S59) was 1:25 (mean dry weight = 16.43 mg), while the lowest yield was recorded at 100% seawater treatment (6.97 mg).

The statistical analysis of the results of this experiment (following SNEDECOR and COCHREN, 1968) show that:

(1) The effect of both soil types on the growth of *Puccinellia* and *Festuca* plants (estimated from mean leaf length) is highly significant (L.S.D. = 5% = 0.8 − 1% = 1.07). (2) The effects of different dilutions of seawater on the growth of both species, estimated from mean leaf length, are highly significant (L.S.D. = 5% = 0.53 − 1% = 0.71). This also became apparent using dry weights as a growth parameter (L.S.D. = 5% = 1.39 − 1% = 1.85). (3) The common effect of both soil types and the different dilutions of seawater on the growth of both species, estimated from the leaf length, is highly significant (L.S.D. 5% = 0.22 − 1% = 0.71). This was also confirmed by mean of dry weights of both species (L.S.D. 5% = 0.8 − 1% = 2.62). (4) The interaction between soil types, the different dilutions of seawater and vegetative fields of both species is highly significant using either mean leaf length (L.S.D. 5% = 0.7 − 1% = 1.0) or the mean dry weights (L.S D 5% = 2.79 − 1% = 3.7) as growth parameters for both species.

Experiment 2: free drainage and waterlogging

These experiments were designed to estimate the importance of inundation by seawater as a controlling factor in the zonation of *Puccinellia* and *Festuca* in the marsh. Which water regimes enable *Puccinellia* to compete with *Festuca* were also of interest.

(a) Seedlings from the marsh. In this series of experiments *Puccinellia* and *Festuca* plants were grown at different water regimes. Fifty large pots filled with *Puccinellia* soil were used. The drainage holes of forty pots were resealed while those of the remaining ten pots (Group V) were left free. In the free drainage experiment, drainage holes were made in two groups each of ten sealed pots at 3 cm (Group I) and 10 cm (Group II) below soil surface. Tap water was applied from above once a day. On the water logging experiment, three groups of ten pots each were used in Group III where the water level was maintained at 3 cm below soil surface whereas in Group IV, the water level was maintained at the bottom (pots with free drainage holes). In the latter case, tap water was applied from above once a day. Harvests were made after six and ten weeks.

The results (Table 3a) are summarized as follows: (1) *Puccinellia* plants showed vigorous growth (mean dry weight = 203.6 mg) when the soil was almost covered with water (Group III), *Festuca* seedlings showed the lowest mean dry weights (10.1 mg) under the same conditions. The differences between the two means (193.5 mg) was high compared with other cases. (2) In the free drainage experiment, the growth of the two species was better in pots of Group I than in Group II. (3) In the water logging experiment, the highest *Puccinellia* dry weight was recorded in Group III in both harvests. The lowest dry weights were in the first harvest of Group V and the second harvest of Group IV. (4) Generally, the yield of *Puccinellia* was higher than *Festuca*. (5) The differences between the yields of the first and the second harvests were very high for all water regimes for *Puccinellia* plants whereas they were low for *Festuca* plants. These observations are confirmed statistically using the correlation coefficient r value (POOLE, 1974). Posi-

Table 3. *Experiment 2: The growth of* Puccinellia maritima *and* Festuca rubra *under waterlogging and free drainage conditions*

Seedlings:	(a) Collected from the marsh																			(b) Germinated in lab			
	Free Drainage								Waterlogging											Water level maintained at 3 cm below soil surface			
	P		F		P		F		P		F		P		F		P		P	P		F	
	M	L	M	L	M	L	M	L	M	L	M	L	M	L	M	L	M	L	M	M	L	M	L
	Group I				Group II				Group III				Group IV				Group V						
Harvesting I 4/28/1967 (6 wks growth)	24.5 ±2.5	4.82	7.00 ±1.02	2.3	17.0 ±1.5	4.58	6.00 ±0.78	1.0	52.8 ± 4.5	9.30	7.10 ±0.76	2.40	19.1 ±2.4	4.50	6.40 ±0.86	1.5	13.9 ±1.2	4.35	5.9 ±0.5	13.6 ±1.2	0.3	2.86 ±0.28	2.0
Harvesting II 5/19/1967 (9 wks growth)	66.5 ±7.8	6.72	11.6 ±1.8	3.4	56.5 ±6.7	6.17	9.50 ±0.09	3.1	203.6 ±11.8	11.82	10.1 ±2.5	2.32	72.7 ±4.06	8.43	5.80 ±0.8	1.5	78.7 ±4.80	9.4	6.80 ±0.8				

M = mean oven dry weight (mgm) L = mean leaf length (cm) P = *Puccinellia* F = *Festuca*

Table 4. *Experiment 3: Response of* Puccinellia *and* Festuca *to different plant nutrients*

(a) Application of nutrients in sand culture

Puccinellia maritima						*Festuca rubra*					
+NP		−P		−N		+NP		−P		−N	
M	L	M	L	M	L	M	L	M	L	M	L
55.1 ±4.1	23.1	39.6 ±3.7	20.0	17.5 ±1.9	0.8	22.6 ±1.7	10.7	22.4 ±2.7	10.06	7.60 ±1.2	0.6

(b) Application of −P nutrient + different dilutions of sea water in sand and soil cultures

Seawater	*Puccinellia maritima*				*Festuca rubra*			
	Soil		Sand		Soil		Sand	
Dilutions	M	L	M	L	M	L	M	L
1:100 ±12.6	98.4	9.6 ±4.5	20.5	4.22 ±11.7	75.1	8.25 ±0.96	8.4	2.94
1:50 ±14.5	124.8	10.3 ±2.9	25.9	5.45 ±14.4	98.0	8.61 ±1.42	9.6	2.94
1:25 ± 8.9	82.1	8.7 ±2.8	26.6	4.5 ±10.2	70.0	7.33 ±1.9	12.9	3.61
1:10 ± 9.0	76.4	9.2 ±3.5	28.6	4.56 ±12.1	57.0	8.00 ±1.27	13.6	3.56
1:2 ± 6.3	49.8	7.07 ±3.17	32.3	5.60 ± 9.9	40.0	6.50 ±1.16	14.9	3.41
100% ± 3.9	43.3	7.0 ±2.19	36.7	5.22 ± 5.4	16.8	5.30 ±2.8	12.7	4.83

M = mean oven dry weight (mgm)
L = mean leaf length (cm)

Table 5a. *Results of competition between* Puccinellia maritima *and* Festuca rubra *for plant nutrients in soil and sand cultures in the presence of different dilutions of seawater. (a) Harvesting I (6 weeks growth)*

Seawater Dilutions	*Puccinellia*				*Festuca*			
	Sand		Soil		Sand		Soil	
	M	L	M	L	M	L	M	L
	(i) Application of complete plant nutrient (+NP):							
1:100	18.5 ± 1.60	5.63	18.1 ± 2.00	9.96	9.10± 1.20	4.25	8.00± 1.30	6.58
1:50	19.4 ± 2.00	6.42	16.9 ± 2.10	8.37	8.90± 1.30	4.457	7.70± 1.40	5.50
1:25	23.1 ± 1.60	6.67	20.2 + 1.70	6.41	8.80+ 1.20	5.47	5.40± 0.40	3.60
1:10	17.1 ± 1.50	5.29	12.5 + 1.30	5.75	8.30+ 1.20	3.68	4.60± 0.30	3.36
1:2	22.3 ± 6.32	16.32	11.5 ± 1.00	8.00	9.30± 0.70	4.00	4.30± 0.30	3.11
100%	22.9 ± 1.10	6.52	10.7 + 1.70	5.32	9.50+ 0.70	3.65	3.60± 0.50	1.94
	(ii) Application of nitrogen-deficient plant nutrient (−N):							
1:100	11.0 ± 0.68	2.88	4.9 ± 3.00	6.96	5.45+ 0.58	2.50	6.58± 0.67	5.86
1:50	9.5 ± 0.75	2.58	12.6 ± 1.30	6.79	4.45+ 0.40	2.09	7.15± 1.00	4.13
1:25	10.7 ± 0.96	3.00	13.8 ± 1.20	6.63	4.00+ 0.56	1.90	6.25± 0.67	4.00
1:10	7.95± 0.31	2.16	12.3 ± 1.24	5.71	4.45± 0.54	1.83	5.00+ 0.96	3.19
1:2	11.0 ± 0.66	2.88	11.8 + 1.04	5.46	4.25+ 0.62	1.70	5.00± 0.64	2.15
100%	9.36± 0.64	3.00	10.6 ± 0.95	4.77	4.05+ 0.32	1.88	4.80± 0.70	2.00

Table 5b. *Harvesting II (10 weeks growth)*

Seawater Dilutions	*Puccinellia*				*Festuca*			
	Sand		Soil		Sand		Soil	
	M	L	M	L	M	L	M	L
	(i) Application of complete plant nutrient (+NP):							
1:100	153.7 ±12.7	7.92	169.5 +14.7	11.88	49.5 ± 5.00	5.18	48.3 ±10.00	8.29
1:50	191.9 ±12.4	9.17	115.5 +13.2	11.97	68.7 ± 7.80	7.46	18.5 + 3.60	9.96
1:25	193.0 ±12.7	8.38	165.3 +16.2	13.30	97.2 + 4.17	7.50	23.2 ± 5.17	8.50
1:10	185.7 ±13.7	8.68	09.4 + 7.4	9.95	60.3 + 4.80	6.80	21.5 ± 4.60	7.90
1:2	194.4 ±11.2	8.79	69.7 + 8.14	9.95	66.3 + 4.80	6.80	21.5 ± 4.60	7.90
100%	209.1 ±10.2	8.75	39.8 + 4.67	9.15	57.1 ± 2.80	6.80	15.4 + 2.80	4.15
	(ii) Application of nitrogen-deficient plant nutrient (−N):							
1:100	12.4 ± 0.78	2.00	81.5 ±12.0	8.66	9.0 + 1.00	1.86	14.6 ± 0.42	4.75
1:50	15.4 ± 1.10	2.10	60.8 + 7.40	6.79	9.0 + 0.80	1.90	10.9 ± 0.96	5.00
1:25	12.5 ± 1.00	2.50	61.4 ± 6.70	8.60	7.2 + 0.50	2.22	9.5 ± 0.98	4.46
1:10	14.2 + 1.80	2.30	85.4 ± 6.60	8.80	8.0 ± 0.60	2.21	27.2 + 5.30	6.14
1:2	18.7 ± 1.53	2.80	46.5 + 5.50	8.90	10.6 + 1.00	2.55	19.1 ± 3.40	5.25
100%	14.8 ± 1.10	2.48	40.2 + 5.30	8.00	6.2 + 0.60	1.60	9.6 ± 2.30	7.40

Table 5c. *Harvesting III (14 weeks growth)*

Seawater Dilutions	*Puccinellia*				*0Festuca*			
	Sand		Soil		Sand		Soil	
	M	L	M	L	M	L	M	L
	(i) Application of complete plant nutrient (+NP):							
1:100	618.3 +23.6	10.8	482.7 ±48.1	14.0	197.8 ±35.9	8.50	99.8 ± 2.90	13.25
1:50	501.3 ±26.3	11.7	504.1 ±46.9	16.3	287.3 ±53.0	8.25	45.4 ± 2.20	10.50
1:25	412.0 ±22.8	12.8	490.9 ±39.5	16.5	257.5 +20.3	13.00	39.9 ± 3.90	12.80
1:10	420.0 ±16.9	10.5	416.8 ±38.4	17.2	236.7 +13.2	12.25	29.4 ± 7.20	9.00
1:2	423.0 ±18.9	11.0	448.3 ±33.6	17.7	249.4 +66.5	9.70	21.3 ± 3.10	12.20
100%	400.0 ±23.6	9.9	280.9 ±21.8	14.2	170.1 +16.7	8.25	10.0 ± 2.10	8.00
	(ii) Application of nitrogen-deficient plant nutrient (−N):							
1:100	20.9 ± 3.40	2.7	188.4 ±45.5	9.4	11.0 + 1.20	2.0	35.5 ± 5.27	7.8
1:50	18.0 ± 1.30	2.1	124.5 ±20.2	9.2	11.1 ± 1.00	1.9	19.8 + 2.38	2.0
1:25	18.3 ± 3.20	2.5	85.4 ±10.7	6.7	11.2 ± 1.10	2.5	21.3 + 3.00	6.7
1:10	19.2 ± 2.10	2.5	140.0 ±11.8	7.8	10.8 ± 1.40	2.4	16.4 ± 0.53	2.3
1:2	22.2 ± 2.20	2.8	123.7 +10.1	9.0	13.4 + 1.00	2.5	13.6 ± 0.78	5.5
100%	17.6 ± 2.60	3.2	101.1 ± 8.10	8.5	9.9 + 0.90	1.8	4.5 ± 0.50	500

M= mean oven dry weight (mgm)
L= mean leaf length (cm)

tive correlation was assessed between the vegetative yields of *Puccinellia* plants (r = +0.85) and waterlogging, the correlation was negative (r = −0.5) for *Festuca* plants.

(b) Seedlings germinated in the lab. The drainage holes of fifteen large pots filled with *Puccinellia* soil were sealed. New holes were made 3 cm below soil surface. Twenty-five seedlings of *Puccinellia* and *Festuca* (both marsh plants and inland variety S59) were transplanted in the pots (5 seedlings of each species in a pot). The pots were immersed in a basin filled with tap water up to the level of the holes. After four weeks the plants were harvested and their dry weights estimared. Results given in Table 3b indicate that: (1) All *Puccinellia* plants grew well (mean dry weights were 13.6 mg, mean leaf lengths were 0.3 cm, relatively higher and longer than other species). (2) All seedlines of the inland *Festuca* S59 died at the end of the experiment. (3) Most of *Festuca* marsh seedlings (60%) died at the end of the experiment. The yield of the survivors was relatively low (mean dry weight = 2.86 mg and mean leaf length = 0.20 cm).

Experiment 3: Response to mineral nutrients

In this experiment, mineral nutrient solutions (Arnon diluted 1:5) were applied to three groups of sand pots (six large sized pots in each group: three for each of the two species). One group was supplied with the complete (+NP) nutrient (500 ml for each pot), the second group with phosphorus-free (−P) nutrient (500 ml for each pot) and the third one with nitrogen-free (−N) nutrient (500 ml for each pot) solutions. Five *Puccinellia* and *Festuca* (marsh) seedlings were transplanted in each pot. The experiment lasted ten weeks and the pots were watered alternately with the appropriate nutrient solution and distilled water.

The experiment was extended to further clarify results. The phosphorus-deficient nutrient solution (−P) was applied (500 ml for each pot to 72 pots, 36 filled with sand and 36 filled with *Festuca* soil). Thc pots were then divided into six groups of twelve pots (six filled with sand and six with *Festuca* soil). Each of the six dilutions of seawater (as per Experiment 1) was applied to one group of pots (300 ml for each pot). Six seedlings of both species were transplanted to each pot. Watering with distilled water and with the phosphorus-deficient solution (−P) was alternated. The plants were harvested after five weeks.

The results are summarized in Table 4. It might be concluded that the two grasses showed a great response to nitrogen because their growth was vigorous when treated with the complete nutrient (55.1 mg and 22.6 mg for *Puccinellia* and *Festuca*, respectively). The nitrogen-deficient nutrient reduced the growth of *Festuca* to about one third (17.5 mg and 7.6 mg). Phosphorus-deficient nutrient had a negligible effect on the growth of *Festuca rubra* (dry weight = 22.4 mg) but produced a relatively marked effect on the growth of *Puccinellia* (dry weight = 39.6 mg).

When treatments of phosphorus-deficient nutrient solutions along with seawater dilutions were applied (Table 4), the soil culture, compared to the sand culture, favoured the growth of both species. The successive increases in salinity (more than 1:50) decreased yields, especially for *Festuca* seedlings, which were less tolerant to high salt concentrations. In the sand cultures, increased salinities caused a slight rise in yield. Seawater thus supplied nutrient to the plants, *i. e.*, the sand culture lacks nutrients necessary for their growth.

Significant correlations were deduced between the vegetative yields of both *Puccinellia* (r = +0.7) and *Festuca* (r = +0.65) and the presence of nitrogen in the nutrient solutions.

Experiment 4: Competition

In each of 60 large pots (30 filled with silvery sand and 30 filled with *Festuca* soil), 6 *Puccinellia* and 6 *Festuca* seedlings (one of each in a hole) were transplanted and treated with 500 ml of complete (+NP) nutrient. Seawater dilutions were applied (each 300 ml) to 5 sand and 5 *Festuca* soil pots. A similar set of 60 pots was treated with nitrogen deficient (−N) solution (each with 300 ml) and seawater dilutions (each with 300 ml) The same number of *Puccinellia* and *Festuca* seedlings were transplanted (6 of each in a pot). The experiment continued for 14 weeks during which the pots were treated alternately with distilled water and nutrient solutions. Ten pairs of pots for each treatment were harvested after 6, 10 and 14 weeks. The results of this experiment (Table 5a, 5b and 5c) show the following:

(1) Both species responded significantly to the complete nutrient as indicated from their increased dry weights. (2) Growth was greater in sand cultures that were treated with complete nutrient. In the *Festuca* soil culture treated with −N nutrient, the mean oven dry weights of both species were relatively greater than those from sand pots. (3) The

successive increases in dry weights was greater for *Puccinellia* plants than for *Festuca* plants. This might explain the degree to which *Puccinellia* seedlings competed for nutrients with *Festuca*. (4) The differences between *Puccinellia* and *Festuca* dry weights were greater for seedlings grown in soil culture than those in sand culture. (5) Successive increases in seawater dilution suppressed the growth of *Festuca* plants more than *Puccinellia*. This effect was more obvious in soil cultures.

Experiment 5: water culture

The solutions of water culture were mixtures of complete nutrient (+NP) and dilutions of seawater (3:1 by volume, respectively). The pH of the solutions ranged between 5.6 and 6.2. Duplicate polythene containers with dark coloured walls were prepared for each of the six seawater dilutions. In each of the containers, 6 seedlings of *Puccinellia* and 6 seedlings of *Festuca* were planted. The seedlings were supported with waxy polystyrene discs. The experiment continued for 10 weeks before the plants were harvested.

The results of this experiment (Table 6) show the wide differences between the yields of the two species. The dry weights of the *Festuca* seedlings were less than 1/5 of those of *Puccinellia*. Higher salinity of seawater solutions (1:2 and 100%) decreased the yields of both species, but the decrease was greater among *Festuca* plants. Also, the leaf length of both species were shortest with 100% seawater treatment.

Table 6. *Experiment 5: Growth of* Puccinellia *and* Festuca *in water culture (+NP nutrient solution + different dilutions of seawater).*

Seawater dilutions	*Puccinellia maritima*		*Festuca rubra*	
	M	L	M	L
1:100	327.0±62.8	12.4	35.4±10.7	4.00
1:50	309.0±66.5	11.7	91.9±22.6	6.60
1:25	323.1±50.2	12.6	81.7±20.2	6.60
1:10	269.5±43.2	11.54	73.7±28.4	5.08
1:2	272.7±38.3	11.13	32.6± 9.5	3.82
100%	146.9±26.5	8.48	19.9± 6.9	3.50

M = mean oven weight (mgm)
L = mean leaf length (cm)

Generally, the yield of *Puccinellia* in water culture was greater compared to that of sand and soil cultures for the same treatments. *Festuca* plants did not show remarkable differences in sand cultures (*cf.* Tables 4 and 6).

Field Experiments

The reason for zonation of *P. maritima* and *F. rubra* at Bank End marsh became clearer after these results were obtained. Two field experiments in the Bank End marsh (May-July 1967) helped establish the final conclusions.

Experiment 1

Two quadrants (each 1 m^2) were selected in each of the *Puccinellia* and *Festuca* zones at Bank End marsh. In each quadrant the plants at 16 spots (13 cm^2) were removed and all soil thoroughly cleaned from the rootlets. Transplantation was effected in the *Puccinellia* zone as follows: 160 *Puccinellia* seedlings were transplanted to the 16 spots in each of the two *Festuca* quadrants (10 seedlings in each spot), and 160 *Festuca* seedlings were transplanted to the spots of the two *Puccinellia* quadrants (10 ssedlings in each spot). The plants were left to grow under natural conditions for 70 days (May 2, 1967-July 10, 1967).

By the end of the experiment, 80% of the *Festuca* plants in the *Puccinellia* zone had died (survivors were weak and yellowish in colour). In the *Festuca* zone, on the other hand, the *Puccinellia* seedlings were still growing (60% growth).

Experiment 2

Twenty tufts (seedlings with soil, 13 cm^2) of *Puccinellia* plants were transplanted to the sites originally occupied by 20 tufts of *Festuca* plants which were, in turn, transplanted to the sites previously occupied by *Puccinellia* tufts. After 4 weeks (May 10, 1967-June 10, 1967), the *Puccinellia* plants were still growing well in the *Festuca* zone. *Festuca* plants became yellowish and many died in the *Puccinellia* zone.

DISCUSSION AND CONCLUSION

The vegetation of the British marshes is organized into ten principal zones (TURRILL, 1962), dominated by the following species, from the sea landward: *Salicornia europaea, Spartina townsendii, Puccinellia maritima, Aster tripolium, Limonium vulgarae, Armeria maritima, Halimione portulacoides, Suaeda fruticosa, Festuca rubra* and *Juncus maritimus.*

At Bank End marsh, the zones between *P. maritima* and *F. rubra* are eliminated. The most landward vegetation zone (*Juncus maritimus*) is poorly represented by depauperate and widely-spaced tussocks of *Juncus*. Elimination of the zones may result from abrupt changes in topographic relief.

These experimental results indicate that the two species, evaluated in terms of total dry-matter production, behave quite differently. Both species showed significant response to N; its absence retarded growth. Although a phosphorus deficiency was less important to *Festuca* growth, the growth of *Puccinellia* was somewhat affected. In general, when the complete nutrient solution was applied, the yield of both species was higher in the silvery sand culture than in the soil culture. When the pots were treated with the nitrogen-free solution, the yield of the plants in the soil pots was higher than that of the sand pots. The soil culture contains plant nutrients with nitrogen that maintain better growth for plants than the silvery sand culture.

The salt tolerance experiment demonstrated that *Puccinellia* has a relatively higher salt tolerance than *Festuca*. This was confirmed by the analysis of the soil samples collected from the zones of both grasses. Soluble sodium in *Puccinellia* soil was higher than that of *Festuca*. Also, the germination experiments indicated that seeds of *Puccinellia* and *Festuca* were likely to grow under various conditions of seawater dilutions (from 1% to 100%) and with NaCl concentration up to 3%. At 4% NaCl, however, *Puccinellia* seeds succeeded in germinating while those of *Festuca* did not. Perusal of Tables 3 and 6 shows a wide difference between the yields of both species when their seedlings were waterlogged or grown in water culture. In the free drainage experiment, or in the cases where the soil was not completely covered with water, *Puccinellia* yields were also higher than those of *Festuca* but the differences were not great.

As regards competition, the yield of *Puccinellia* was higher under the two treatments of plant nutrients (+NP and −N) and in the two cultures (soil and sand) than that of *Festuca*. The differences between their yields became wider as the amount of seawater increased in the solutions applied to the pots, especially at 50% and 100% seawater. This seems to suggest that *Festuca* fails to compete with *Puccinellia* under high salinity conditions.

The results of germination and growth experiments clarified the problem of zonation of Bank End marsh, but as they were conducted under controlled conditions, it was necessary to set up experiments in the field under natural growth conditions for *Puccinellia* and *Festuca*. The transplanted *Festuca* seedlings failed to grow in the *Puccinellia* zone (a long period of tidal inundation), while *Puccinellia* seedlings survived in the *Festuca* zone (a short period of tidal inundation).

TURRILL (1962) states that "the flora [of the marshlands] is limited to those plants which can withstand high salinity and non-considerable degree of fluctuation in this salinity, for parts of the salt marsh have seawater concentrated to saturation in a dry spell or diluted in a rainy spell". *Puccinellia* and *Festuca* are salt marsh grasses that tolerate salinity to different extents. A more important factor is evidently flooding by tidal water. *Festuca* plants cannot withstand long periods of tidal floodings in the *Puccinellia* zone.

Another important factor is the topographic relief of the marsh. It was observed at Bank End marsh that the terraces of the *Puccinellia* zone represent small islands delimited by *Festuca* plants. On the other hand, the lower parts and creeks dissecting the *Festuca* zone were dominated by *Puccinellia* plants.

The final conclusion of these experiments and field observations is that the pattern of zonation at Bank End marsh is primarily controlled by tidal inundation and topographic relief. Salinity is also an important factor that plays a secondary role. Thus one may paraphrase from TANSLEY (1953), noting that the zones of the marshes are related only approximately to tidal levels. SOUTHWARD (1958) further states "the range of the tide or amplitude, is usually the major factor governing the verticla range of intertidal zone, and hence the width or height of the various zones of plants and animals."

ACKNOWLEDGEMENTS

The author is grateful to Professor C.D. Pigott, former head of the Department of Botany and Director of the Botanic Garden, Cambridge University, England, for supervising the work. I am also indebted to Professor W. Kassas, Faculty of Science, Cairo University and Prof. A.I. Naguib, Academy of Scientific Research and Technology, Cairo, for reading the manuscript.

LITERATURE CITED

BUTCHER, R.W., 1961. *A New Illustrated British Flora*. London: Leon Hill, 1,080p.

CLAPHAM, A.R.; TUTIN, T.G. and WARBURG, E.F., 1962. *Flora of the British Isles*. Cambridge: Cambridge University Press, 1,591p.

POOLE, R.W., 1974. *An Introduction to Quantitative Ecology*. New York: McGraw-Hill, 532p.

SNEDECOR, G.W. and COCHREN, W.G., 1968. *Statistical Methods.* Ames, Iowa: Iowa State University Press, 593p.

SOUTHWARD, A.J., 1958. The zonation of plants and animals on rocky shores. *Biological Review,* 33, 137-177.

TANSLEY, A.G., 1953. *Types of British Vegetation.* Cambridge: Cambridge University Press, 970p.

TURRILL, W.B., 1962. *British Plant Life.* London: Collins St. James, 315p.

□ RESUMEN □

Este articulo presenta un estudio ecofisiológico de los comunidades en marismas marinas: *Puccinellia maritima* y *Festuca rubra.* Estas dominan la segunda y tercera zona de la marisma Bank End en el Irish Sea, en el noroeste de Inglaterra. Se han realizado tres tipos de experimentos, germinación, invernadero y campo, respuesta a nutrientes minerales y tolerancia a la salinidad. Los resultados de la experimentación indican que una combinación de factores (marea, relieve, salinidad del suelo, *etc.*) controla la zonación de las dos comunidades pero diferiendo sus efectos individuales. El movimiento mareal y el relieve son los factores ambientales principales. La salinidad parece que en este caso juega un papel de menor importancia. La deficiencia de nitrógeno es básica en el crecimiento de ambas especies. La ausencia de fósforo origina un ligero descenso del crecimiento.--*Miguel A. Losada, Universidad de Cantabria, Santander, Spain*

□ ZUSAMMENFASSUNG □

In diesem Vortrag wird eine ökophysiologische Forschung von zwei Sumpfengräser (*Puccinellia maritima* und *Festuca rubra*) durchgeführt. Diese Spezies vorherrschen die zweite und dritte Zonen vom Bank End-Sumpf (nordwestliche Küste Grossbritanniens, auf dem Irischen Meer). Drei Versuchstypen (Keimen-, Gewächshaus-und Feldversuchen) wurden durchgeführt, um mehr über die Zonationmüster, die Erwiderungen auf Mineralnahrung und den Salzwiderstand zu entdecken. Die Ergebnisse dieser Versuchen zeigen, dass viele kombinierte Umstände (z.b. Flutbewegungen, Bodensalzgehalt, Erleichterung) die Zonation der zwei Pflanzgemeinden beherrschen; einzelne Wirkungen unterschieden sich jedoch. Flutbewegungen und Bodenerleichterung sind wichtige umweltbedingte Umstände. Weil beide Spezies salzwiderstandfähig sind, und die Bodensalzgehälte von den beiden Gemeinden fast vergleichbar sind, scheint der Salzgehalt relativ unwichtig zu sein. Ein Stickstoffmangel beschädligt den beiden Spezies; wenn der Phosphor fehlt, gibt es ein kleinerer Ertrag.--*Stephen A. Murdock, CERF, Charlottesville, Virginia, USA*