

Vegetation structure of TMAP vegetation types on mainland salt marshes

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1. Introduction

The structure of vegetation has a strong impact on habitat characteristics and ecological processes. Barkman (1979) specifies direct and indirect effects of vegetation structure, for example, influences on germination and establishment of plant species, as well as the creation of microhabitats through differences in temperature, wind, precipitation, light and radiation. Vegetation structure modifies trophic interactions, most obviously on the level of plant-herbivore interactions. Arthropod diversity and abundance (Denno and Roderick, 1991) and grazing preferences of herbivorous geese (van der Graaf *et al.*, 2002; Bos *et al.*, 2005) depend on vegetation structure, but also perceived predation risks and habitat selection of breeding birds (Whittingham and Evans, 2004). Thyen and Exo (2005) and Norris *et al.* (1998) found a significant relationship between agricultural land use and breeding densities of redshank *Tringa totanus* on salt marshes. This was mainly due to the impacts of agricultural land use on the structure and zonation of vegetation. It is suggested that vegetation structure is an important factor for redshank reproduction through provisioning of suitable nesting localities (Thyen and Exo, 2005).

The Trilateral Monitoring and Assessment Program (TMAP), implemented in 1997, is the most important monitoring system in the Wadden-Sea area. The aim is to provide a scientific assessment of the status and development of the Wadden Sea ecosystem, and to assess the status of implementation of the trilateral targets of the Wadden-Sea Plan. One important part of the TMAP is the monitoring of salt marsh areas to provide a comprehensive inventory. To synchronise the vegetation mapping in the three countries involved (The Netherlands, Denmark, Germany), the TMAP vegetation types for salt marshes were defined by an expert panel and first published in the Quality Status Report 2004 (Bakker *et al.*, 2005). Nowadays, virtually all vegetation maps of salt marshes in the TMAP region are based on this typology. However little is known about the structural parameters of the TMAP vegetation types.

The characterisation of the vegetation structure according to the different TMAP vegetation types will provide a tool for extracting information on vegetation structure from available TMAP vegetation maps with the potential of extrapolating data on vegetation structure for most of the international Wadden-Sea region.

The aim of this study is a comparison of different TMAP vegetation types in salt-marsh communities with respect to various parameters of vegetation structure. As previous studies on the vegetation structure of salt marshes identified human land use as a parameter of prime importance (Andresen, 1990; Bakker and de Vries, 1992; Kiehl, 1997), we compared the influence of different types of management (mown, grazed and fallow) on the vegetation structure of the TMAP vegetation types, and assessed the seasonal variation within one growing season.

While the ecological importance of vegetation structure is widely acknowledged in literature, a variable use of definitions and the absence of measuring standards hamper the comparability of studies (*cf.* Zehm, 2006). In our approach, we apply different methods of analysis of vegetation structure to make progress in the search for a standardised method.

2. Methods

2.1 Study area

The study was conducted on mainland salt marshes along the German Wadden Sea coast of Lower Saxony (National Park 'Niedersächsisches Wattenmeer'). All study sites fall within the TMAP area and are mapped regularly within the trilateral monitoring. Data for this study were gathered at three locations: 'Jadebusen' with mown, fallow and grazed salt marshes (N 53° 24'; E 8° 8'), 'Norderland' with grazed and fallow sites (N 53° 40'; E 7° 21') and 'Leybucht' with grazed and fallow sites (N 53° 30'; E 7° 6'). Elevation of the study sites ranged from 1.10 m above sea level (ASL) up to 2.99 m. Grazing intensities are approx. one (head of) cattle per ha. Grazing takes place from end of April till mid October. The mown areas are mown

Table 1:
TMAP vegetation types
analysed in this study.

TMAP code	TMAP vegetation type
S 1.2	Pioneer zone, <i>Salicornia</i> type
S 2.1	Low marsh, <i>Puccinellia maritima</i> type
S 2.4	Low marsh, <i>Atriplex portolacoides</i> type
S 3.0	High marsh, unspecific
S 3.3	High marsh, <i>Festuca rubra</i> type
S 3.5	High marsh, <i>Artemisia maritima</i> type
S 3.7	High marsh, <i>Elymus</i> ssp. Type
S 3.9	High marsh, <i>Atriplex</i> ssp. Type

once a year after the 1st of July and fallow sites have remained without any agricultural land use for at least 20 years. Data were pooled for all sites as there were no significant differences in vegetation structure between the three locations.

2.2 Sampling design

We used random stratified sampling to generate measuring points within each study site (approx. three sample points per ha). Stratification was done according to the latest TMAP vegetation map available. The main measuring period was from the end of June until the beginning of August 2007. To analyse seasonal changes, additional measurements were done for part of the data set between mid April and mid May 2007.

Vegetation data were collected at each plot in a percentage abundance scale. All plot data were classified according to TMAP vegetation types (Bakker *et al.*, 2005; Table 1).

For the definition of vegetations structure we followed Zehm *et al.* (2003) and distinguished vertical (elements in side view) and horizontal structure (*i.e.* light penetration).

Vertical vegetation structure was analysed with a standardized photographic method. At 297 points, we took digital photographs of the

vegetation as described in Zehm *et al.* (2003). The software tool SIDELOOK (Nobis, 2005) calculates spatial parameters of the vegetation by analyzing the 'vegetation-pixels' within each photograph. Analysis follows Zehm *et al.* (2003).

Horizontal vegetation structure was measured at 279 points by means of a PAR (400-700 nm) sensor (SunScan, Delta-T Devices Ltd., 1m - array with 64 light sensors). The light incidence at soil level (light penetration through the vegetation) is expressed as a percentage of the light intensity above the canopy. At 178 points we calculated from the 64 light sensors (on a light sensitive surface of 100 cm x 1 cm) the spread of light reaching the soil, as a value for vegetation heterogeneity. All parameters analysed in this study are listed in Table 2.

2.3 Statistical analyses

Data were checked for heteroscedasticity with the Fligner-Killeen test of homogeneity of variances. With no significant differences in variance, we applied one-way ANOVAs and for multiple comparisons Tukey's 'Honest Significant Difference' post-hoc comparison of means with a 95% family-wise confidence level. With significant differences in variance present, we used the Kruskal-Wallis rank sum test and for multiple comparisons the Mann-Whitney U test with Holm correction.

For the analyses of the seasonal development of vegetation structure, we calculated the change per sample point over time and divided this value by the number of days between the two measurements ('slope').

All statistical analyses were done using the R statistical software (R Development Core Team 2008).

Table 2:
Parameters analysed in this
study.

Parameter (codes)	Definition
Incidence of light [%] (incidence.PAR)	Light (PAR) reaching the soil surface, expressed as percentage of the light intensity above the canopy
Spread of light (spread.PAR)	Spread of the 64 light measurements (PAR) at the soil surface with a light sensitive surface of 100 cm x 1 cm
Mean column density [%] (mean.density)	Mean vegetation density calculated from densities per column (10 cm wide stripes of the picture analysed)
Difference of the column densities [%] (diff.density)	Difference of the lowest and highest density per column (10 cm wide stripes of the picture analysed)
Maximum canopy height [cm] (max.height)	Maximum height of the vegetation within each picture
Difference of the column heights [cm] (diff.height)	Difference between the maximum heights per column (10 cm wide stripes of the picture analysed)
Top-line length (tl.length)	Length of the line running along the crest of the highest plant elements divided by the width of the analysed picture
Height reaching specific percentage of density [cm] (pc-50 / pc-75)	Height below which 50% / 75% of the vegetation density is located
Row density [%] (rdX-Y)	Density of vegetation in an area between X and Y cm above the soil surface (10 cm wide rows of the picture)

		Light measurement				Photographic method / column and global parameters							
		N	incidence.PAR	N	spread.PAR	N	mean.density	diff.density	max.height	diff.height	tl.length	pc-50	pc-75
grazed	S 1.2	5	0.49±0.25	5	0.41±0.20	6	23.53±14.46	6.57±1.80	42.75±21.40	14.9±6.68	5.75±1.58	13.48±5.00	20.03±7.81
	S 2.1	13	0.72±0.14	13	0.19±0.14	37	18.35±8.96	4.96±4.36	30.35±17.75	8.04±6.33	4.62±1.61	9.47±4.53	14.27±7.01
	S 3.0	14	0.57±0.20	13	0.27±0.15	22	19.12±5.05	4.57±3.31	34.16±12.46	12.23±10.54	5.52±1.67	9.68±2.48	14.65±3.77
	S 3.3		NA		NA	7	20.95±8.89	8.64±5.88	39.10±19.00	14.1±7.61	4.67±0.72	10.76±4.44	16.47±7.05
	S 3.5	7	0.31±0.17	7	0.70±0.25	7	36.61±4.67	13.23±6.66	51.64±7.28	11.81±7.48	4.51±0.94	18.36±2.33	28.29±3.39
	S 3.7	7	0.19±0.06	6	0.88±0.14	34	40.14±7.75	9.77±4.51	69.07±14.04	18.4±9.35	3.72±1.36	20.91±4.30	32.34±6.55
fallow	S 2.1	78	0.23±0.18	39	0.67±0.27	65	31.77±6.73	11.44±7.64	54.65±18.65	14.15±12.99	4.97±1.56	17.04±3.79	27.04±8.05
	S 2.4	24	0.14±0.09	20	1.11±0.53	21	36.93±6.66	7.63±7.72	52.67±8.29	9.31±4.43	4.25±0.84	18.76±3.14	28.68±4.83
	S 3.3	14	0.15±0.09	6	1.03±0.11	9	38.82±5.96	14.43±5.16	63.12±18.50	19.04±15.53	4.21±0.96	20.1±3.07	31.30±5.92
	S 3.7	53	0.15±0.15	28	0.98±0.36	34	41.52±8.04	11.78±6.44	71.59±17.89	14.15±12.12	5.18±2.63	22.81±7.91	36.32±11.04
	S 3.9	23	0.19±0.21	12	0.86±0.35	17	40.49±9.48	19.71±8.99	73.89±20.72	21.76±13.37	6.14±3.81	22.53±5.07	35.84±8.35
	S 3.9	23	0.19±0.21	12	0.86±0.35	17	40.49±9.48	19.71±8.99	73.89±20.72	21.76±13.37	6.14±3.81	22.53±5.07	35.84±8.35
mown	S 2.1	15	0.37±0.15	15	0.43±0.21	15	33.11±7.25	9.03±6.58	47.11±11.48	8.05±5.59	5.41±0.92	16.83±3.71	26.00±6.17
	S 3.7	22	0.20±0.24	14	0.68±0.31	18	53.72±10.70	16.64±8.37	94.85±17.24	15.13±7.77	6.41±2.29	28.76±5.90	45.79±8.85

Table 3: Means, standard deviations and sample sizes of the analysed parameters of vegetation structure. TMAP codes see Table 1, parameter abbreviations and units see Table 2; NA – not available.

		Photographic method / row parameters: Row density										
		N	rd0-10	rd10-20	rd20-30	rd30-40	rd40-50	rd50-60	rd60-70	rd70-80	rd80-90	rd90-100
grazed	S 1.2	6	84.02±37.84	74.72±36.05	45.08±45.15	22.3±31.77	6.58±13.52	2.00±4.90	0.60±1.47	0.35±0.86	0±0	0±0
	S 2.1	37	96.06±4.94	53.53±38.80	22.72±33.94	8.23±16.22	2.43±6.35	0.77±2.76	0.19±0.74	0.03±0.16	0±0	0±0
	S 3.0	22	99.05±1.61	70.89±32.89	18.99±16.64	2.27±4.04	0.46±1.34	0.02±0.07	0±0	0±0	0±0	0±0
	S 3.3	7	96.81±3.11	65.1±39.05	34.29±33.29	10.86±15.52	2.10±3.73	0.54±0.94	0.13±0.34	0±0	0±0	0±0
	S 3.5	7	100±0	99.40±0.75	85.63±15.40	60.64±19.91	18.10±13.22	2.46±4.99	0.11±0.30	0±0	0±0	0±0
	S 3.7	34	98.57±4.30	94.80±6.87	84.59±13.66	65.73±22.52	36.99±25.39	13.7±15.27	4.60±7.63	1.90±5.36	0.71±2.08	0.20±0.71
fallow	S 2.1	65	96.14±5.63	89.01±12.67	71.77±20.27	39.78±24.05	11.89±12.57	3.44±7.82	1.83±6.55	1.54±5.79	1.22±4.67	1.13±4.71
	S 2.4	21	99.17±3.16	97.29±7.15	88.63±12.26	57.73±25.06	22.00±23.33	4.54±11.19	0.30±0.70	0±0	0±0	0±0
	S 3.3	9	98.67±2.60	95.29±7.23	89.12±7.24	62.88±13.88	27.51±17.75	7.89±14.05	3.44±9.92	1.51±4.53	0.77±2.30	0.78±2.33
	S 3.7	34	96.28±15.55	93.26±14.29	84.83±16.22	63.54±23.34	37.02±23.95	19.15±19.42	10.59±17.66	7.33±18.12	2.87±7.58	0.74±2.27
	S 3.9	17	94.71±8.56	87.11±16.10	80.21±13.79	61.01±19.03	38.65±23.90	21.92±20.14	12.91±14.44	5.74±8.50	2.11±4.18	0.57±1.42
	S 3.9	17	94.71±8.56	87.11±16.10	80.21±13.79	61.01±19.03	38.65±23.90	21.92±20.14	12.91±14.44	5.74±8.50	2.11±4.18	0.57±1.42
mown	S 2.1	15	99.27±2.34	96.41±4.87	75.16±24.90	42.23±29.79	14.33±17.65	2.94±8.68	0.99±3.82	0.09±0.34	0±0	0±0
	S 3.7	18	96.59±7.46	95.49±7.01	87.22±10.44	78.25±11.29	64.79±18.41	46.38±26.14	30.63±22.89	19.28±18.50	10.61±11.38	5.36±7.82

3. Results

For each analysed TMAP vegetation type (Table 1) the mean and standard deviation of vegetation structure characteristics per agricultural land use scheme were calculated (Table 3).

An analysis of vegetation structure on fallow sites mirrored the natural variation between TMAP types without human disturbance. For the incidence of light and the top-line length we

found no significant differences between the TMAP vegetation types on fallow sites (Table 4). However, the most distinct differences occurred between the TMAP vegetation types S 2.1 (Low marsh, *Puccinellia maritima* type) and S 3.7 (High marsh, *Elymus* ssp. type), with the latter being significantly higher, denser and more heterogeneous (Table 3 and 4). But also S 2.1 and S 3.9 (High marsh, *Atriplex* ssp. type) differed significantly for

	Incidence of light (U)	Spread of light (U)	Mean column density	Difference of the column densities (U)	Maximum canopy height	Difference of the column heights (U)	Top-line length	Height reaching 50 % of density	Height reaching 75 % of density (U)
S 2.4 - S 2.1	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.3 - S 2.1	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.7 - S 2.1	n.s.	**	***	n.s.	***	n.s.	n.s.	***	***
S 3.9 - S 2.1	n.s.	n.s.	***	**	**	n.s.	n.s.	**	**
S 3.3 - S 2.4	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.7 - S 2.4	n.s.	n.s.	n.s.	*	**	n.s.	n.s.	*	*
S 3.9 - S 2.4	n.s.	n.s.	n.s.	***	**	**	n.s.	n.s.	n.s.
S 3.7 - S 3.3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.9 - S 3.3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.9 - S 3.7	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.

Table 4: Levels of significance for differences between the TMAP vegetation types on fallow sites. Given are the p-values according to Tukey's HSD or Mann-Whitney U test (U). *** p ≤ 0.001; ** p ≤ 0.01; * p ≤ 0.05; n.s. not significant. For TMAP codes see Table 1.

Figure 1: Row density of different heights above the soil surface for S 2.1 (Low marsh, *Puccinellia maritima* type) and S 3.7 (High marsh, *Elymus ssp.* type) on fallow sites.

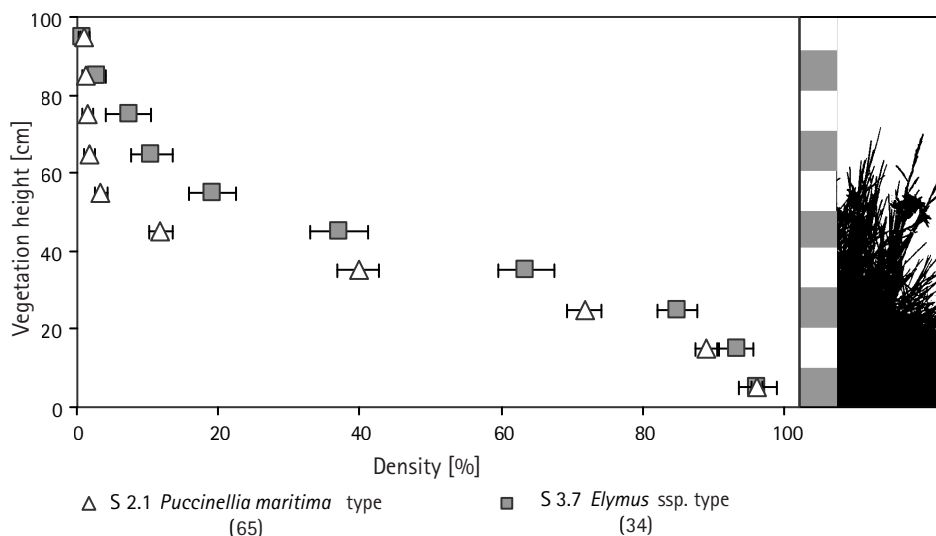


Table 5: Influence of agricultural land use on vegetation structure of different TMAP vegetation types. Shown are the levels of significance of ANOVA or Kruskal-Wallis rank sum test (K) calculated for each TMAP vegetation type with more than one agricultural land use schemes (Table 3). *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; n.s. not significant; NA - not available. For TMAP codes see Table 1.

	Incidence of light	Spread of light	Mean column density	Difference of the column densities	Maximum canopy height	Difference of the column heights	Top-line length	Height reaching 50 % of density	Height reaching 75 % of density
S 2.1	***	***	***	*** (K)	***	**	n.s.	***	***
S 3.3	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	**
S 3.7	n.s.	*	***	**	***	n.s.	***	***	***
S 3.9	NA	NA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

five different parameters of vegetation structure (Table 4).

At all canopy heights, the *Elymus ssp.* type (S 3.7) was significantly denser than the *Puccinellia maritima* type (S 2.1) except for the lowest 10 cm. Above 70 cm, vegetation density approached values of zero for both types (Figure 1 and Table 3).

Additional analyses focused on the influence of agricultural land-use schemes on vegetation structure. Grazing and mowing as management tools on salt marshes had a strong impact on the structure of TMAP vegetation types investigated: on grazed sites the canopy height was lower and the vegetation was less dense than on fallow sites (Table 3).

When comparing structural components of the two focal TMAP vegetation types *Puccinellia maritima* type and *Elymus ssp.* type (S 2.1 and S 3.7, respectively), we again found less dense vegetation on mown as compared to fallow sites (Figure 2), but for the *Elymus ssp.* type the canopy was significantly higher on mown than on fallow sites ($p < 0.001$; Table 3).

Agricultural land use had a strong and significant impact on most of the structural parameters

investigated for the TMAP vegetation types S 2.1 (Low marsh, *Puccinellia maritima* type), S 3.3 (High marsh, *Festuca rubra* type) and S 3.7 (High marsh, *Elymus ssp.* type), whereas there was no significant impact on TMAP vegetation type S 3.9 (High marsh, *Atriplex ssp.* type; Table 5).

As can be expected, we found a very consistent seasonal decline of light at soil level for all land-use schemes. This is attributable to the closing of canopies as the growing season progresses (Figure 3). However, this decline was significantly steeper on mown than on grazed or fallow sites for both focal TMAP vegetation types S 2.1 (*Puccinellia maritima* type) and S 3.7 (*Elymus ssp.* type).

Spatial grazing patterns and forage avoidance by cattle create strong differences in light availability between a *Puccinellia maritima* type (open and short canopy) and an *Elymus ssp.* type (large amounts of standing dead vegetation early in season; Figure 3 left panels top and bottom).

4. Discussion

Vegetation structure is an important determinant of habitat quality, influencing various ecological processes such as seed germination, predator

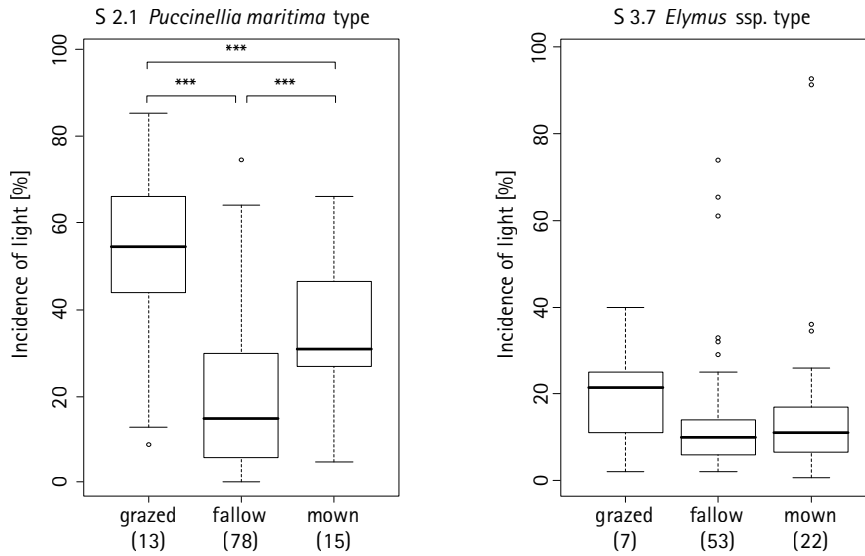


Figure 2: Influence of agricultural land use on the incidence of light. Shown are the TMAP vegetation types S 2.1 and S 3.7 (ANOVA S 2.1 $p < 0.001$ ***; S 3.7 $p = 0.49$).

escape and foraging efficiency. Our knowledge of the mechanisms behind these processes is still fragmentary, especially with regard to the influence of plant structure on higher trophic levels, i.e. herbivores and predators. Our study aims at providing necessary background information on vegetation structure of salt-marsh plant communities in order to facilitate further research on plant-herbivore and predator-prey interactions.

This study characterises vegetation structure for the most common TMAP vegetation types

on mainland salt marshes (Table 1). Supported by the statistically significant differences found between focal TMAP vegetation types in different land-use schemes, it will be possible to extrapolate our findings to TMAP areas where vegetation mapping provides information on the occurrence of TMAP vegetation types and land-use, and to deduce information on vegetation structure for these areas.

As previous studies (Andresen, 1990; Bakker and de Vries, 1992; Kiehl, 1997) have already

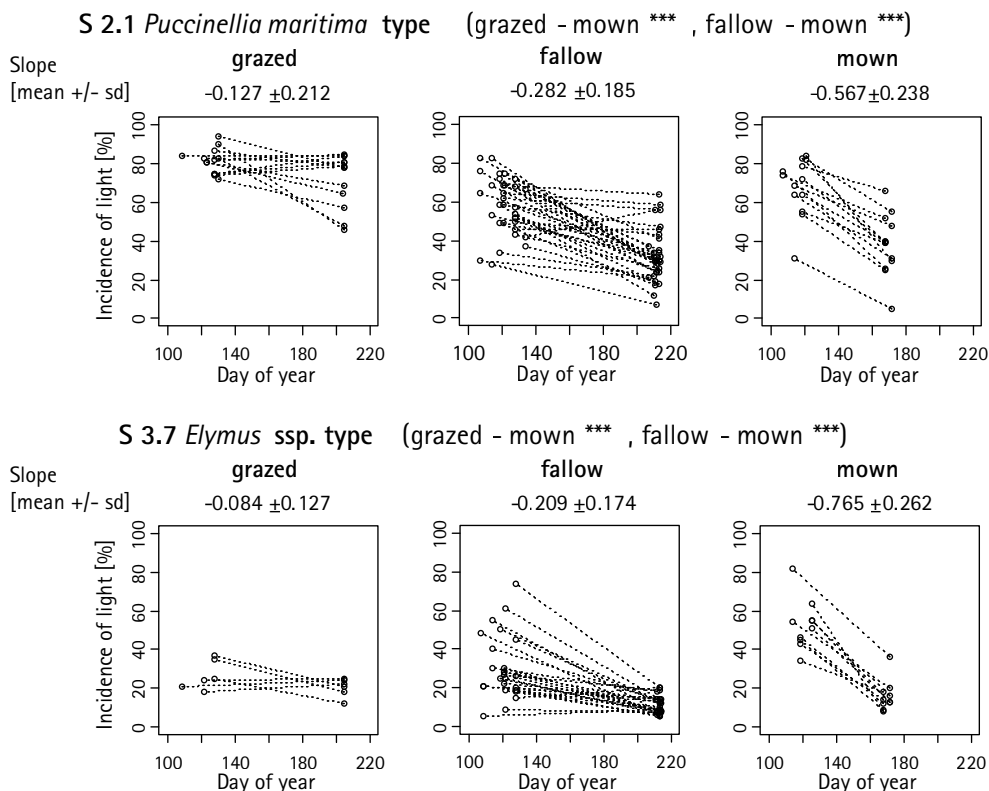


Figure 3: Seasonal development of incidence of light in different land use schemes for two focal TMAP vegetation types. *** $p \leq 0.001$.

suggested, our data confirm the strong impact of grazing and mowing on structural vegetation parameters, specifically canopy height and sward density. For an even more complete description of the structure of TMAP salt marsh vegetation, we suggest that future studies focus on a comparison of mainland and island salt marshes, as well as on inter-annual variation, with repeated measurements in different years.

Seasonal change of the vegetation structure attributable to plant growth is an important component and needs to be taken into account; especially when results are to be transferred to other regions. Therefore, it is necessary to conduct repeated measurements throughout the growing season at the same plots. Our study provides repeated measurements for only a few sample points, but already these first results demonstrate the strong influence of agricultural land use on the development of vegetation structure during the period of plant growth.

In this study, we used two largely differing methods for the analyses of the vegetation structure. On the one hand, a quick assessment of the overall horizontal density of vegetation through light measurements, and on the other hand, the very detailed method of picture analyses in order to assess vertical structure. Both methods are suitable to obtain information about vegetation structure, but provide different parameters. As is often the case in ecological studies, the method of choice depends on the questions asked: for studies on the germination of seeds, the incidence of light is a suitable parameter (Bakker and de Vries, 1992), while for the occurrence of arthropods a more detailed analysis on the density of vegetation in different canopy heights (cf. Figure 1) will be necessary.

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