Interactions between *Limonium vulgare* and *Plantago maritima* in the *Plantagini-Limonietum* on the Boschplaat, Terschelling, The Netherlands*

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Abstract

Limonium vulgare and *Plantago maritima* are growing together over large areas and in varying proportions on the Boschplaat salt marsh. The question is how both species interact and which environmental factors play a role in those interactions.

There are indications of different measures of niche differentiation in the *Plantagini-Limonietum* association related to differences in flooding frequency and substrate. Interactions between both species are described according to three models (related to de Wit's competition model). Mechanisms that may cause niche differentiation are: differences in growth rhythm, in salt tolerance, in rooting depth, in preference to types of substrate, in morphology, in mycorrhizae and diseases.

On a small scale (spatial heterogeneity in the marsh and variation in subsequent seasons) *Limonium* can achieve a bigger portion in the vegetation by occupying open sites faster than *Plantago*. On a larger scale (the whole marsh, decades) the impossibility of *Plantago* to germinate and rejuvenate after sedimentation of silt and salinisation of the soil is the determining factor causing an overall decrease of this species (compared with *Limonium*) and increase of *Limonium*.

The life cycle of both species, criteria for scale in space and time, and the question whether the *Plantagini-Limonietum* should be considered a syntaxon, are discussed.

Introduction

Studies on interactions between *Limonium vulgare* and *Plantago maritima* were carried out in plant communities on the tidal salt marsh of the

Boschplaat, a 4400 ha nature reserve. This area is situated at the east side of the Frisian island of Terschelling (Fig. 1).

Until 1930 the Boschplaat was an almost bare sand flat except for six isolated dune complexes in the south covered with vegetation.

Between 1931 and 1936 a sand barrier was constructed running along the north side of the Boschplaat. Since then the area is only flooded by water from the Wadden Sea. This resulted in accretion of silt and the development of a salt-marsh vegetation over large parts of the former sand flats (Westhoff, 1947).

Phytocoenoses with *Limonium* and *Plantago* have been assigned to the *Plantagini-Limonietum* by Westhoff & den Held (1969). This vegetation
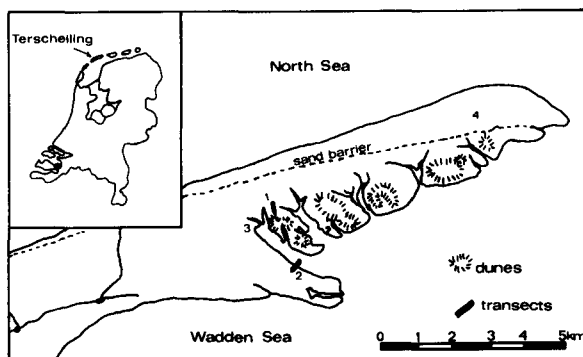
Fig. 1. Terschelling, Boschplaat. Location of the four areas. For explanation of the numbers see the text.

type is considered a transition between the haline sand and the haline silt series (Roozen & Westhoff, 1984). In succession this association is preceded by the *Puccinellietum maritimae parapholietosum* and the *Plantago maritima* sociation (both belonging to the sand series), and followed by the *Armerio-Festucetum* (sand series) or the *Plantagini-Limonietum* terminal stage, and the *Artemisietum maritimae* (both belonging to the silt series). Apart from these succession lines, another line has been recognised running from the *Puccinellietum maritimae typicum* via the *Limonium vulgare* sociation to the *Artemisietum maritimae* association (silt series).

Limonium and *Plantago* are both species with a clonal growth form. Both have rhizomes with rosettes, which die off in autumn. *Limonium* has a more or less 'guerilla' growth form and *Plantago* a 'phalanx' growth form (Harper, 1978). In this stage of succession growth is more important for both species than reproduction. The rosette (ramet: Harper & White, 1974; White, 1979) is taken as a modular unit in this study.

An aim was to see whether models constructed for studying interactions between species in agriculture, like de Wit's model (de Wit, 1960) and other related models (Braakhekke, 1980; Berendse, 1981; Spitters, 1983a, b), could be applied on species in natural ecosystems.

The general hypothesis was that coexistence and changes in the *Limonium/ Plantago* ratio is caused by competition, which is influenced by flooding, soil formation and related processes.

For the different plant communities in which both species share, some hypotheses were deve-

loped based upon the transitional position of the *Plantagini-Limonietum* between the sand and silt series:

   a. In the *Limonium vulgare* sociation (Roozen & Westhoff, 1985; 111.0 ± 0.4 cm above Dutch Ordnance Level; transect 1) *Limonium* is excluding *Plantago* (Fig. 2).

   b. In the *Plantagini-Limonietum* (114.6 ± 0.3 cm; transect 1) there is an equilibrium between both species.

   c. In the *Plantago maritima* sociation (117.0 ± 0.2 cm; transect 1) *Plantago* is excluding *Limonium* (Fig. 2).

   d. In the *Plantagini-Limonietum* terminal stage (119.0 ± 0.5 cm; transect 2) *Limonium* is excluding *Plantago* (Fig. 3).

Materials and methods

The plant communities mentioned on three sites have been studied (see Fig. 1).

1. Transect 1 was laid out perpendicular to the vegetation zonation in 1953 (see also Roozen & Westhoff, 1985). It is only flooded during exceptionally high tides. A silt layer of 5-10 cm has been deposited.

2. Transect 2 was also laid out in 1953 (Roozen & Westhoff, 1985) and is flooded regularly. A silt layer of 10-20 cm has been formed.

3. Besides these transects an area (no. 3, Fig. 1) studied since 1968 by Ketner (1972), and a part of the beach plain north of the sand barrier (no. 4, Fig. 1), were used for additional data.

The transects were divided into permanent plots and recorded with irregular intervals during the last 30 years.

In July 1980, 70 respectively 55 plots of 10 × 10 cm in the *Limonium vulgare* and *Plantago maritima* sociations were chosen at random, and the rosettes of *Limonium* and *Plantago* and aerial parts of other species present were harvested. In the *Plantagini-Limonietum* terminal stage 50 and in the *Plantagini-Limonietum* in area 3 (Fig. 1) 30 such plots were sampled. In almost all other plant communities along the transects 15 such squares have been sampled. Numbers of modular units (individuals of annuals, rosettes, tillers of grasses) and dry weights were recorded.
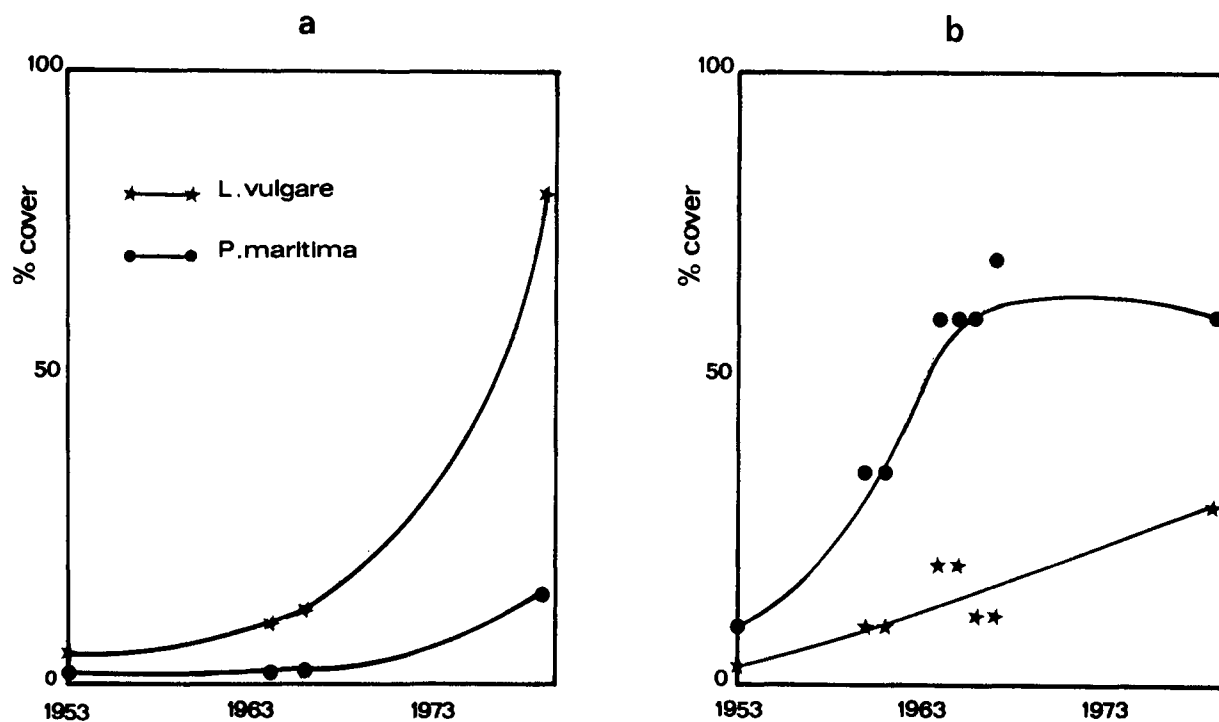
Fig. 2. The change of the cover percentages of *Limonium vulgare* and *Plantago maritima* (1953–1979) in the *Limonium vulgare* (a) and the *Plantago maritima* sociation (b) in transect 1.
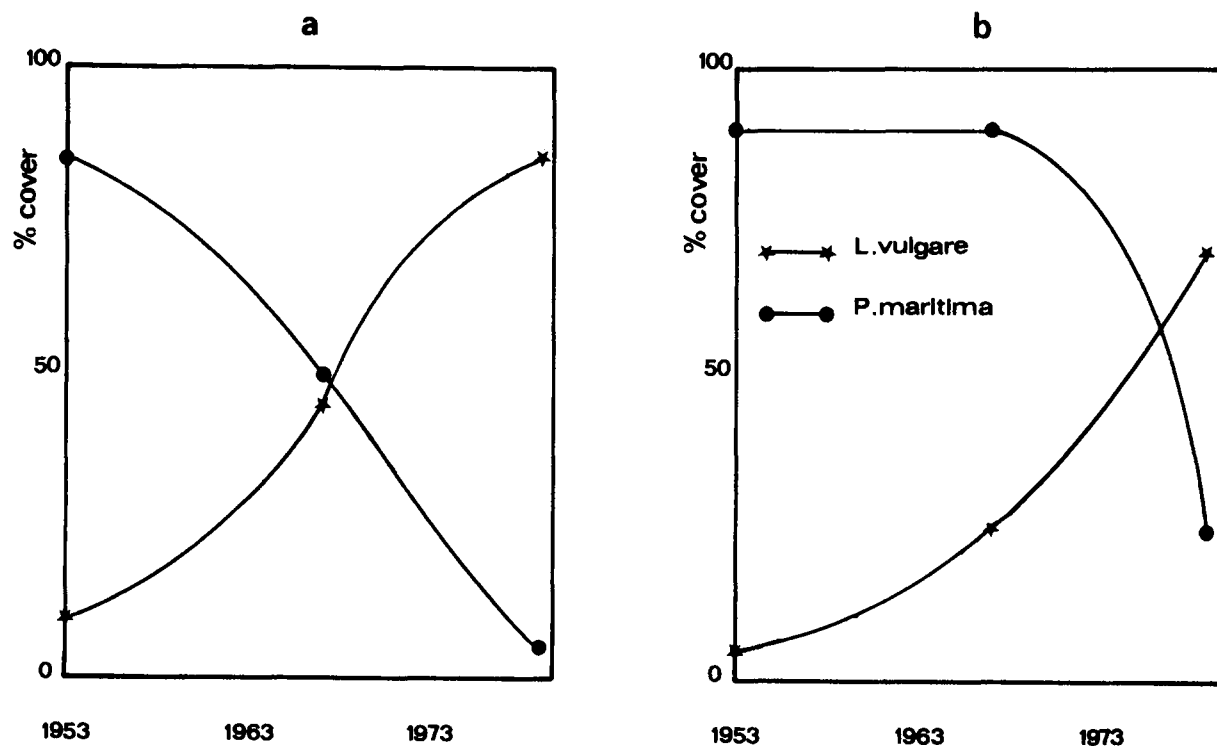

Fig. 3. The change of cover percentages of *Limonium vulgare* and *Plantago maritima* (1953–1979) at two different sites (a, b) in the *Plantago maritima* sociation in transect 2.

To test the hypotheses and to quantify the effects of interactions three models have been used.

1. A hyperbolic model (de Wit, 1960) transformed by Spitters (1983a, b) into a linear regression model:

$$1/W_L = b_L + b_{L,L}N_L + b_{L,P}N_p + \text{covariables} \quad (1)$$

$$1/W_P = b_P + b_{P,P}N_P + b_{P,L}N_L + \text{covariables} \quad (2)$$

in which W_L (W_P) are the rosette weights (g/rosette)
b_L (b_P) are the inverse of the biomasses of isolated rosettes (rosette/g)
$b_{L,L}$ ($b_{P,P}$) are the inverse of intraspecific competition: the competition a rosette experiences from one rosette of the same clone or from another of the same species.
$b_{L,P}$ ($b_{P,L}$) are the inverse of interspecific competition: the competition a rosette experiences from one rosette of another species.
The covariables are similar terms for the other species present in a plant community.

This model assumes that interactions are density independent and that the relative yield total (RYT, van den Bergh, 1968) does not equal one. This fits to field conditions, where species appear in various densities and RYT is not likely to be 1.

2. A linear model:

$$W_L = b_L + b_{L,L}N_L + b_{L,P}N_P + \text{covariables} \quad (3)$$

$$W_P = b_P + b_{P,P}N_P + b_{P,L}N_L + \text{covariables} \quad (4)$$

In this model the curve found when rosette biomass is plotted against rosette density is assumed to be straight.

3. An exponential model:

$$e^{Y_L} = b_L + b_{L,L}N_L + b_{L,P}N_P + \text{covariables} \quad (5)$$

$$e^{Y_P} = b_P + b_{P,P}N_P + b_{P,L}N_L + \text{covariables} \quad (6)$$

In this model the asymptotic exponential relation between biomass per area unit (Y) and rosette density is linearised.
All regression equations can be extended by other terms (covariables).

The relative replacement rate of *Limonium* with regard to *Plantago* (RRR_{LP}), a measure of change in the *Limonium/Plantago* rosette or biomass ratio (de Wit & van den Bergh, 1965; Braakhekke, 1980) has been calculated according to

$$RRR_{LP} = (Y_L/Y_P)_{t+1}/(Y_L/Y_P)_t \quad (7)$$

$$\text{or } \log(Y_L/Y_P)_{t+1} = \log RRR_{LP} + \log(Y_L/Y_P)_t \quad (8)$$

$$\text{or } \log(Y_L/Y_P)_{t+1} = \log RRR_{LP} + \log(N_L/N_P)_t + \log(W_L/W_P)_t \quad (9)$$

in which Y is the biomass of a species per area unit (g · m^2)
N is the rosette density (no. of rosettes · m^2)
W is the rosette dry weight (g)

If $RRR_{LP} > 1$ *Limonium* excludes *Plantago*. $RRR_{LP} = 1$ means an equilibrium state. Cover percentages of both species recorded during the last 30 years in the transect plots are supposed to be proportional to Y (see also Ketner, 1972). The RRR_{LP} per year is calculated according to $\sqrt[n]{RRR_{LP}}$ (n is the number of years), based on the RRR_{LP} value over periods of several years (de Wit & van den Bergh, 1965).

Germination experiments

A germination experiment was carried out with *Plantago* seeds in 0.125 m^2 circular plots, laid out in the *Limonium vulgare* and *Plantago maritima* sociations, where all species present had been removed. In both plant communities there were four series: 100 *Plantago* seeds sown on sand (artificially placed) or silt, and sown superficially in sand or silt.

In addition a germination experiment was carried out in a growth chamber (20 °C, 16 h light) with *Limonium* and *Plantago* seeds on a water potential gradient created by different NaCl solutions (0 to 2 000 mmol NaCl · l⁻¹), whereby 40 seeds of each species were laid out on filter paper in petri dishes.

Growth experiments

Growth experiments on water culture were carried out in a glass-house using 14 days old seedlings of both species in order to establish specific species properties under optimal nutritional conditions at different salt levels (0 to 800 mmol NaCl · l⁻¹). The climate in the glass-house was hardly under control in summer and the glass-house was heated in winter (18 °C, 16 h light). The seedlings (dry weight at the start of the experiment in December: 8.9 mg for *Limonium* and 19.3 mg for *Plantago* on an average) grew in pots on an aerated Steiner solution. The experiment ran for 38 days and there were 5 harvests on day 17, 20, 32, 35 and 38. Each time 5 plants

of each salt level were harvested. Dry weights of shoots and roots were measured, as well as the leaf area. The relative growth rate (RGR), the net assimilation rate (NAR) and the leaf area ratio (LAR) have been calculated according to Hunt (1978).

Results

Figures 4 and 5 show the distribution of the rosette density and the biomass per sq · m of *Limonium* and *Plantago* in the different plant communities along transect 1. The curves have a different shape, illustrating that it depends on the species property measured how it is distributed along the gradient. Examples of such gradients in space and time are given by Beeftink *et al.* (1977) and van der Maarel (1976).

Table 1 shows the RRR_{LP} per year for different periods during the last 30 years in transect 1 and 2. As also can be seen from Figure 2 the portion of biomass of *Limonium* increased compared with that of *Plantago*. The rate of this increase differs per plant community, because of the changing combinations of environmental factors at the different sites resulting in differences in growth rates, death rates of rosettes, etc. (Harper, 1978; Jerling, 1982). In transect 1 the process takes place more slowly than in transect 2. $RRR_{LP} = 1$ can also be interpret-
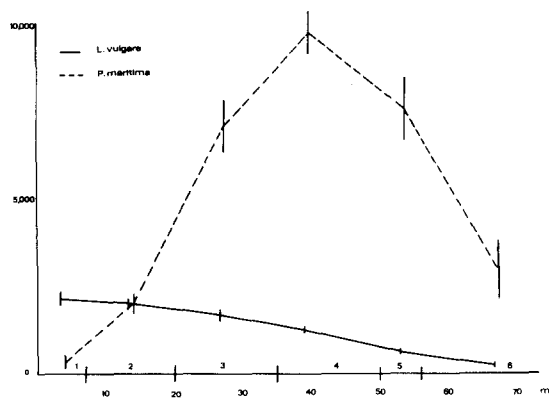

Fig. 5. Rosette biomass (g · m ^{2}) of *Limonium vulgare* and *Plantago* maritima along transect 1 from the lower to the higher salt marsh (July 1980). See Figure 4.

ed that *Limonium* is growing in another microhabitat (depressions) than *Plantago* (elevations), which occurs in the *Limonium vulgare* sociation.

The RRR_{LP} in locality 3 (Fig. 1) is slightly higher than 1, although the value can vary between successive years dependent on variations in environmental factors. The RRR_{LP} becomes more reliable when calculated over longer periods of time (RRR_{LP} (1953–1979)).

Another way to express the RRR_{LP} is shown in Figure 6 (ratio diagrams). The ratio lines (estimated regression lines) for the *Limonium vulgare* sociation and the *Plantagini–Limonietum* terminal stage cross the line $RRR_{LP} = 1$ (equilibrium) in a way Braakhekke (1980) defines as a stable equilibrium. The ratio line for the *Plantago maritima* sociation (Fig. 7) is parallel to and above the diagonal, which means that there exists no equilibrium: *Limonium* excludes *Plantago*. The calculated RRR_{LP}'s (according to formula 9) are 1.04 ('equilibrium' in the *Limonium vulgare* sociation is due to the occupation of both species of different microhabitats), 1.98 (*Limonium* excludes *Plantago* in the *Plantagini–Limonietum* terminal stage while the ratio diagram shows 'equilibrium') and 1.29 (*Limonium* excludes *Plantago* in the *Plantago maritima* sociation).

The contradictions between calculated RRR_{LP}'s and ratio diagrams can firstly be explained by insufficient number of ratios of *Limonium* and *Plantago* growing together in the sample, secondly by the fact that the ratio diagrams are made on an aerial biomass basis only, and finally by the environmental conditions in the summer of 1980, which may be exceptional for the 30 years period (storm flood in April, followed by a period of severe drought in May).

Fig. 4. Number of rosettes per sq · m of *L. vulgare* and *P. maritima* along transect 1 from the lower to the higher salt marsh (July 1980). 1. Zone with *Halimione portulacoides* + *L. vulgare* (height above Dutch Ordnance Level in cm: 113.7 ± 1.9); 2. *Limonium vulgare* sociation (111.0 ± 0.4); 3. *Plantagini-Limonietum* (114.6 ± 0.3); 4. *Plantago maritima* sociation (117.0 ± 0.2); 5. zone with *Juncus maritimus* (123.7 ± 0.5); 6. *Armerio-Festucetum* (130.2 ± 0.4).
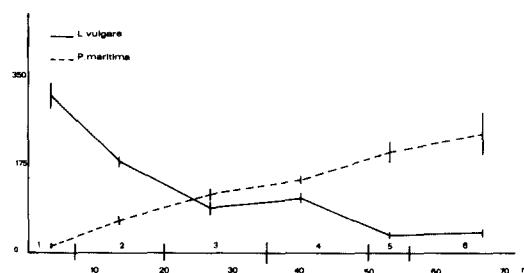
Table 1. Relative replacement rates per year of *Limonium vulgare* and *Plantago maritima* calculated for several periods at different vegetation types in transect 1, 2 and area 3 between 1953 and 1979. See also Figure 1, 2 and 3.

Transect 1

Vegetation in 1979 L. vulgare sociation		Plantagini–Limonietum				P. maritima sociation	
		Lower part		Higher part			
Period	RRR_{LP}	Period	RRR_{LP}	Period	RRR_{LP}	Period	RRR_{LP}
1953–1964	1.07	1953–1966	1.00	1953–1961	0.97	1953–1960	0.96
						1960–1961	1.00
				1961–1966	1.11	1961–1964	1.04
1964–1966	1.12					1964–1965	1.00
						1965 1966	0.58
		1966–1967	0.75	1966–1967	1.06	1966 1967	0.84
1966–1979	1.01	1967–1979	1.07	1967–1979	1.02	1967–1979	1.10
1953 1979	1.04	1953–1979	1.02	1953–1979	1.02	1953–1979	1.01

Transect 2

Vegetation in 1953 P. maritima sociation Vegetation in 1979 L. vulgare + Artemisia maritima		P. maritima sociation L. vulgare + H. portulacoides		Puccinellietum maritimae L. vulgare + H. portulacoides		P. maritima sociation L. vulgare + F. rubra	
Period	RRR_{LP}	Period	RRR_{LP}	Period	RRR_{LP}	Period	RRR_{LP}
1953 1967	1.16	1953–1954	1.92	1953–1955	1.50	1953–1967	1.14
		1954–1955	0.27				
		1955–1957	0.92	1955–1957	0.97		
				1957–1958	0.57		
				1958–1960	1.44		
		1957–1965	1.26	1960–1965	1.00		
		1965–1967	1.22				
1967–1979	1.28	1967–1979	1.20	1965–1979	1.07	1967–1979	1.19
1953 1979	1.21	1953–1979	1.14	1953–1979	1.07	1953–1979	1.16

Area 3

Plantagini–Limonietum	
Period	RRR_{LP}
1968 1969	1.35
1969–1970	0.86
1970–1980	1.09
1968–1980	0.99

100

$\log(Y_L/Y_P)_{t+1}$

classes of vegetation biomass ('pressure')

● 0.00 - 2.00 g.dm^{-2}

✳ 2.00 - 2.50

△ 2.50 - 3.00

□ 3.00 - 5.00

RRR$_{LP}$ = 1

10

1

$y = 0.1157 + 0.8030\,x$

corr. 0.81

$\log(W_L/W_P) = 0.4279$

RRR$_{LP}$ = 1.98

0.1

0.01   0.1   1   10

$\log(N_L/N_P)_t + \log(W_L/W_P)_t$
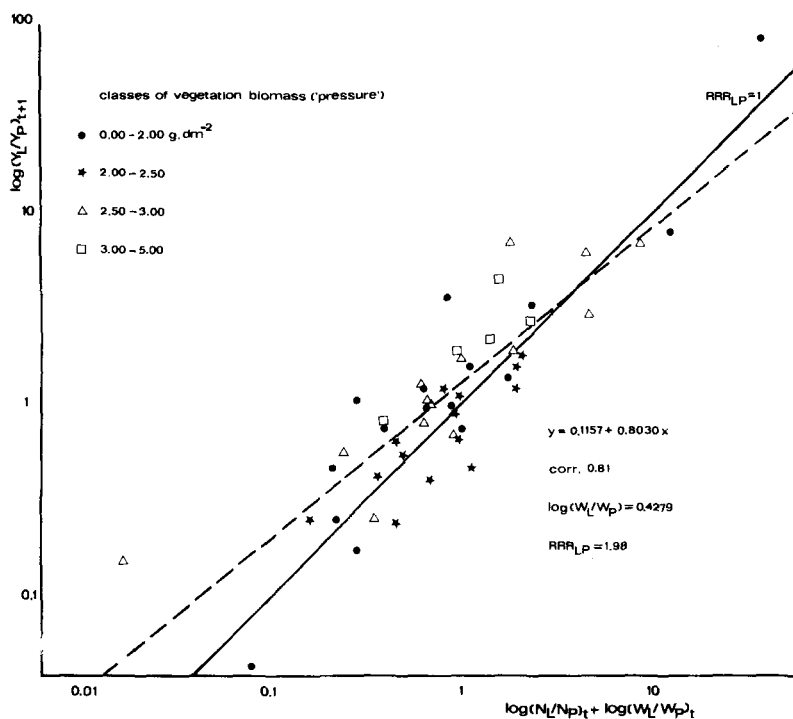
Fig. 6. Ratio diagram for the *Plantagini-Limonietum* terminal stage (transect 2) for the 1980 growing season.

10

$\log(Y_L/Y_P)_{t+1}$

classes of vegetation biomass ('pressure')

● 0.00 - 2.00 g.dm^{-2}

✳ 2.00 - 2.50

△ 2.50 - 3.00

□ 3.00 - 4.00

RRR$_{LP}$ = 1

1

$y = 0.2286 + 0.9839\,x$

corr. 0.88

$\log(W_L/W_P) = 0.4512$

RRR$_{LP}$ = 1.29

0.1

0.01

0.01   0.1   1   10
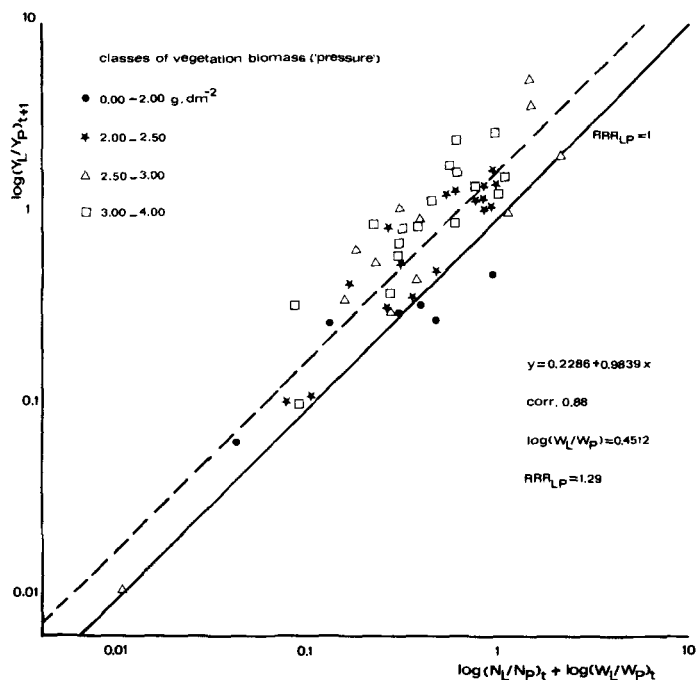
$\log(N_L/N_P)_t + \log(W_L/W_P)_t$

Fig. 7. Ratio diagram for the *Plantago maritima* sociation (transect 1) for the 1980 growing season.

Estimate of competition effects

An estimate of the competition effects is made with the help of the three mentioned models. The results are shown as replacement diagrams (de Wit, 1960) in Figures 8, 9 and 10. These diagrams were constructed by substitution of the regression coefficients (b's in the formulas 1-6) in de Wit's formulas for replacement of species in mixtures (de Wit & Goudriaan, 1978). The resulting curves are calcu-

lated and not based on data recorded in the field.

All models show niche differentiation, but each model is sensitive to a different aspect of it:
- in the linear model (Fig. 8) the effects of intra-specific competition are obvious, especially in those vegetation types where either Limonium or Plantago dominates.
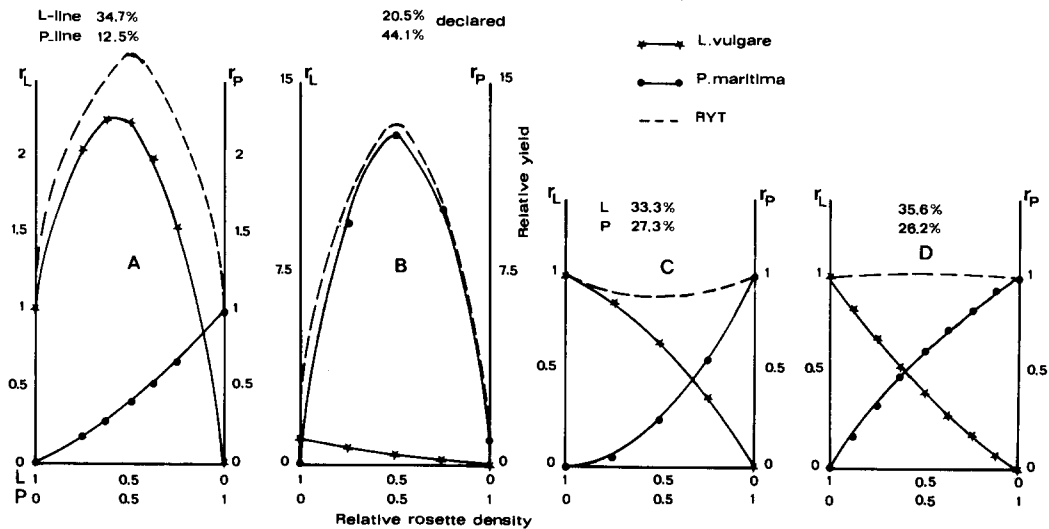- the hyperbolic model (Fig. 9) is more sensitive to mutual interference of both species (concave and convex curves).

Fig. 8. Replacement diagrams of Limonium vulgare and Plantago maritima according to the linear model. A. The Limonium vulgare sociation in transect I with Halimione portulacoides and Salicornia europaea as accompanying species. B. The Plantago maritima sociation in transect 1 with Halimione portulacoides and Aster tripolium. C. The Plantagini-Limonietum terminal stage in transect 2 with Aster tripolium and Salicornia europaea. D. The Plantagini Limonietum in area 3 with Festuca rubra and Aster tripolium. The percentages declared (derived from the regression analysis) are given as well.
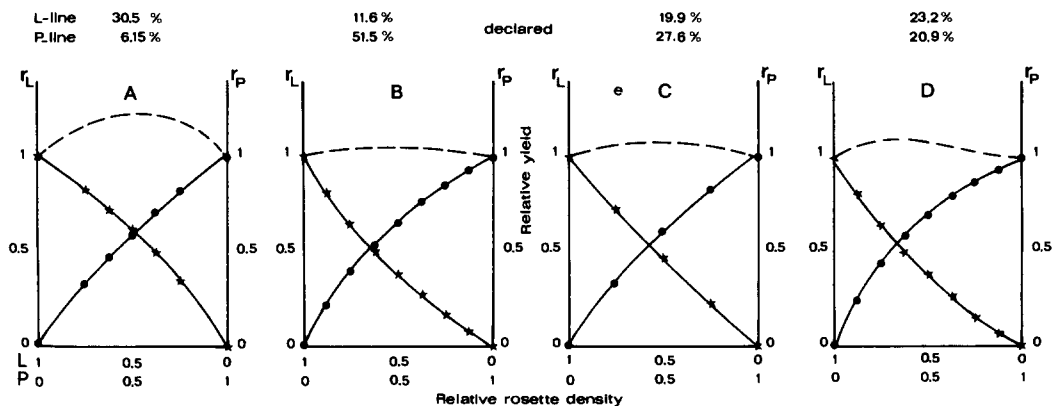

Fig. 9. Replacement diagrams of Limonium vulgare and Plantago maritima according to the hyperbolic model. For explanation of the kind of vegetation types see Figure 8.
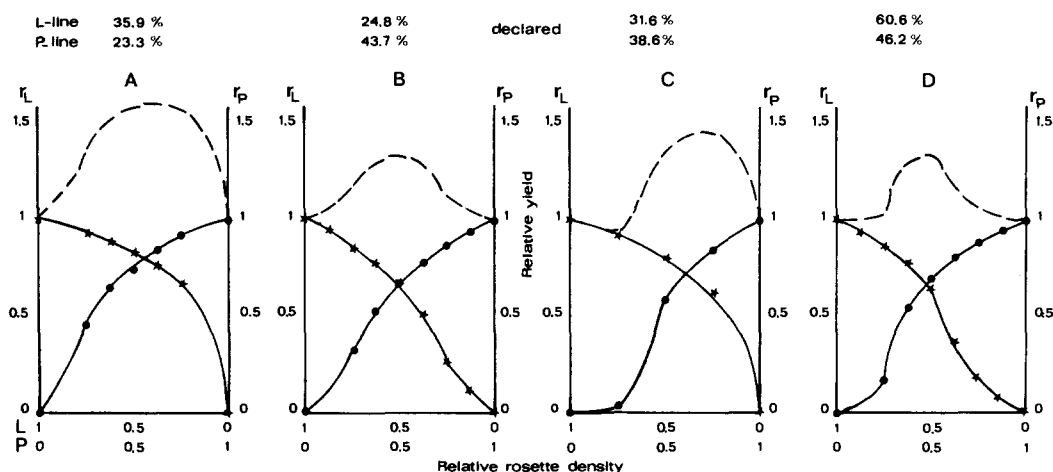
Fig. 10. Replacement diagrams of *Limonium vulgare* and *Plantago maritima* according to the exponential model. For explanation of the kind of vegetation types see Figure 8.

– the exponential model (Fig. 10) shows to be sensitive to density dependence of the species in their 'home' microhabitats (S-shaped curves), for the position of the *RYT* and the range of mixtures within which an equilibrium is possible.

Probably the shape of the curves and the *RYT* values are dependent on the substitution ratio: how many rosettes of one species replace one rosette of the other species?

It should be remembered that all regression models are influenced by:

– interactions between all plant species and individuals: 'competition' for space and nutrients, pathogens (van Leur, 1981) and mycorrhizae (Boullard, 1958).

– the heterogeneity of the environment: microhabitats (Braakhekke, 1980; Berendse, 1981), their spatial and temporal scale, non-random distribution of plants (rosettes) in the environment.

– the size of the sample area as a competition unit, especially in plants with clonal growth (Spitters, pers. comm.).

Germination experiments

In the field *Plantago* germinated only on the sandy substrate (20% of the sown seeds germinated within 14 days in or on sand; 0% germinated in or on silt).

In the growth chamber *Limonium* germinated at higher salt concentrations (up to 800 mmol NaCl·l⁻¹) than *Plantago* (up to 400 mmol NaCl·l⁻¹). These results are in agreement with the process of silt accretion during the rise and fall of the *Plantago* population in some areas (Fig. 2), and are confirmed by the observation that hardly any seedlings of this species occur in the silted area south of the sand barrier, while many were found on the sandy beach plain north of it (Fig. 1). The consequence might be that *Plantago* will disappear from the silted area in the course of time.

Growth experiments

When the salt concentrations increase the *RGR* of *Plantago* decreases to a greater extent than that of *Limonium* (Table 2). The same holds for the *NAR*, while the decrease of the *LAR* is of the same order for both species. It was observed that *Plantago* roots coloured brownish at the higher salt concentrations. It is difficult to apply these results to field situations, because glasshouse conditions are not in accordance with field conditions. At most these results are indicative of specific differences.

Conclusions and discussion

In the *Limonium vulgare* sociation *Plantago* is found on micro-elevations with cover percentages

Table 2. The *RGR* (g·g⁻¹·day⁻¹), the *NAR* (g·cm⁻²·day⁻¹) and the *LAR* (cm²·g⁻¹) of *Limonium vulgare* and *Plantago maritima* at different salt concentrations in the glass-house in September and December 1980.

| | | | | | *Limonium vulgare* | | | | | | |
| September | | | | | December | | | | | | |
NaCl	RGR	% red. RGR	NAR	% red. NAR	NaCl	RGR	% red. RGR	NAR	% red. NAR	LAR	% red. LAR
0	0.094	-	0.0204	-	0	0.039	-	0.1913	-	0.2052	
200	0.089	5.3	0.0201	1.5	600	0.016	59.0	0.1209	36.8	0.1296	36.8
400	0.081	13.8	0.0190	6.9	800	0.020	48.7	0.1912	0.01	0.1059	48.4
					Plantago maritima						
0	0.137	-	0.0120	-	0	0.042		0.2936	-	0.1435	-
200	0.113	17.5	0.0115	4.7	600	0.016	61.9	0.1742	40.7	0.0896	37.6
400	0.082	40.1	0.0091	24.2	800	0.016	61.9	0.1518	46.1	0.0755	47.4

relatively independent of those of *Limonium* (Fig. 2), and *Limonium* in micro-depressions. Consequently there are indications of niche differentiation (Figs. 8, 9 and 10), so the hypothesis for this plant community, that *Limonium* is excluding *Plantago*, is rejected.

- In the higher situated *Plantago maritima* sociation the portion of *Limonium* is slowly increasing. Probably the same happens in the *Plantagini-Limonietum*. The hypothesis for the *Plantago maritima* sociation, that *Plantago* is excluding *Limonium*, is rejected. The hypothesis for the *Plantagini-Limonietum*, that there is an equilibrium between both species, is not rejected.
- The hypothesis for the *Plantagini-Limonietum* terminal stage, that *Limonium* is excluding *Plantago*, is not rejected, because *Plantago* is continuously decreasing in this area and *Limonium* is not.
- In the *Plantagini-Limonietum* in area 3 *Limonium* slowly increases, while the portion of *Plantago* is decreasing in this plant community.
- The growth of *Limonium* is less reduced than that of *Plantago* at higher soil salinities.
- Germination and establishment are dependent on the kind of substrate. *Plantago* germinates only on or in a sandy substrate, and *Limonium* germinates only on or in silt. *Plantago* germinates at lower soil salinities than *Limonium*. Germination and establishment are the most important factors in the change of the *Limonium/Plantago* ratio on a large scale (the whole

marsh, decades), probably followed by the way both species grow on a small scale (spatial heterogeneity, seasonal variation). *Limonium* occupies open sites faster than *Plantago*.

Little is known about the *Limonium* and *Plantago* seed banks. Transport of seeds takes place by the incoming tide, especially to higher parts of the salt marsh (Jerling, 1982). *Plantago* produces many seeds in certain areas, but nothing is known about their fate in the Boschplaat ecosystem. Probably there is no massive germination as is found by Jerling (1982) in Sweden. Germination and establishment are dependent on a coincidence of favourable conditions like light, fresh water, substrate, little inundation, salt and sedimentation (Boorman, 1967; Arnold, 1973; Blom, 1978; Jerling, 1982). This means that there are recruitment years at different sites in different years, which is one of the causes of a reticulate vegetation development (Grubb, 1977; Harper, 1977).

A second important factor in the shift of the *Limonium/Plantago* ratio is probably the specific growth form. In this stage of the succession (the accent for both species is on vegetative growth) redistribution of space (niche differentiation) is probably realised by other species properties such as different rooting depth (*Plantago* roots deeper than *Limonium*), growth rhythm (differences in *RGR*, separated in time within the growing season, especially caused by the varying soil salinity, and in flowering (Ketner, 1972; Jerling, 1982)), morphological salt-tolerance mechanisms (*Plantago*: suc-

culence; *Limonium*: salt glands), physiological mechanisms (osmotics; Stewart *et al.*, 1979), mycorrhizae, pathogens, animals.

Abiotic environmental factors causing a change in redistribution of space can be light (Jerling, 1982), fresh water conditions, mineralisation (Beeftink *et al.*, 1978), humus content, nitrogen and phosphate concentrations. These factors influence the size of rosettes and individuals (Jefferies, 1977; Jefferies & Perkins, 1977).

Environmental factors and genetic differences influence the growth parameters in various ways at different sites and different times. Therefore, Burdon & Harper (1980) plead for examining *RGR* differences between and within natural populations, and not for determining average *RGR* differences between species only (Grime, 1979), to trace biotic selection mechanisms (Turkington & Harper, 1979; Burdon, 1980; Harper, 1982).

On account of these differences and factors it is difficult to say whether the changes in the *Limonium/Plantago* ratio are caused by competition or not. These changes are primarily a result of physical factors causing *Limonium* succeeds *Plantago* with a considerable overlap in time (see also Simberloff, 1982). These factors in their turn might be determined by vegetation.

The *Plantagini–Limonietum* is an association occurring in the transition between the haline sand and silt series. The question remains whether it is a distinct plant community or a large boundary of the *Limonium vulgare* and *Plantago maritima* sociations. And if it must be considered a distinct plant community, what are then its boundaries, spatial and temporal (van der Maarel, 1967)? So far, criteria for plant communities have been species composition, abundance and cover percentages. These are reflections of environmental conditions. Changes in these properties are caused by natural selection of individuals of species as reactions to stimuli from the environment (Harper, 1982). Interactions between species are determined by the spatial and temporal scale of environmental heterogeneity. The result is an ever changing vegetation pattern. Maybe some other criteria can be added to those already mentioned which enable us to define a plant community more strictly (or not, because we cannot measure the immeasurable).

For such oligo-specific communities other criteria like species pattern, the completeness in which the species fulfil their life cycles, and the life time of the whole plant community should be taken into account as well. The latter parameter can be measured according to the age distribution of the composing species, cover percentages or biomass determinations and will vary per site (Beeftink, 1979). Therefore, long term research integrating vegetation science, population biology and ecophysiology is necessary.

However, the danger exists that only the measurable and testable phenomena will be recognised as the only existing. Nature, a plant community and a plant or animal are more than that. So behind all those measured phenomena (figures, tables and formulas) the Boschplaat hides itself as a beautiful, large and quiet area where people can feel themselves part of nature.

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