Vegetation study as a generator for population biological and physiological research on salt marshes*

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Abstract

The paper deals with some views on the phytocoenose in relation to the functioning of vegetation and its plant-species populations in space and time. From these viewpoints the study of vegetation is seen as a field of tension between the organismic and reductionistic approaches. Both have their value, provided any dogmatism is avoided and either can be applied to the other.

In the field of vegetation structure characteristic features of life-form spectra and species distribution, inversion phenomena in zonation, and community architecture in relation to production and decomposition are discussed. In this connection some remarks are made on habitat and niche differentiation with respect to the phytocoenose concept.

Vegetation dynamics are discussed in relation to the introduction of *Spartina anglica*, the frequency of flooding by the tides, different environmental disturbances caused by heavy winter frost, rainfall and hot and dry periods, as well as to human interferences for agricultural and civil-technical purposes.

It is suggested that salt-marsh plants may have found refuge areas in inland habitats as well as on more southerly coastal sites during glaciations.

General considerations

The object of vegetation science is the multi-species plant cover as a (semi)natural entity and its relation to the environment, especially soil and climate. Vegetation is considered an ensemble of plant communities separated from each other, either by more or less sharp boundaries or shading off into each other by relatively broad transition zones (van Leeuwen, 1966; van der Maarel, 1976).

There is a variety of theoretical views on the nature of plant communities. Most of them are 'organismic', viz. view the plant community as an entity with certain analogies to an organism (Clements, 1916, 1928; Tansley, 1935; 'quasi-organismic'). Another organismic view was presented as a taxonomic analogy. Especially Braun-Blanquet (1928, 1932) had in mind that just like organisms are classified into a hierarchy of taxonomic groups, communities can be arranged in a hierarchical system. Students of this tradition usually subdivide vegetation study into a number of 'syn'-approaches, derived from equivalent sections of botany (for instance Braun-Blanquet, 1928, 1932; Westhoff, 1970): synecology, syndynamics, synchorology, synphysiology, synmorphology, and syntaxonomy or synsystematics. This parallelism in terminology suggests close relationships between studies on both integration levels.

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* Nomenclature follows Tutin *et al.* (1964–1980).

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Contrary to these organismic views Gleason (1926, 1939) posed his 'individualistic' or 'reductionistic' concept of the plant community. He emphasized the dynamic nature of the plant community as an expression of these selective forces of its particular environment and the surrounding vegetation, and he considered the community a changeable mixture of principally independently distributed plant species. From this view Whittaker (1953, 1957, 1967) came to the concept of the plant community as a complex population pattern and as the result of a number of interacting species populations.

This paradigmatic dispute will not be treated here in full (see e.g. Westhoff, 1951, 1970; Whittaker, 1962; Braun-Blanquet, 1964; Westhoff & van der Maarel, 1973; Mueller-Dombois & Ellenberg, 1974; McIntosh, 1980; van der Maarel, 1984). It is illustrated only that in the course of time these views are converging in refining and extending the definition of basic concepts for making them more operational for ecological research.

First, in the beginning there were misunderstandings on whether a plant community is a concrete or an abstract unit. Westhoff (1951) proposed to separate them by using the terms phytocoenose and phytocoenon (as a specification of the general term coenon introduced by Barkman *et al.* (1958)).

Secondly, an evolution in the definition of the phytocoenose concept developed from the more superficial 'any collection of plants growing together which has as a whole a certain unity' (Tansley, 1935) to the more useful 'a part of the vegetation consisting of interacting populations growing in a relatively uniform environment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation' (Westhoff & van der Maarel, 1973). Although uniformity is considered a relative concept in this definition permitting some subjectivity in delimiting a phytocoenose, the introduction of the population structure of vegetation admits the phytocoenose to be conceived as a system of interacting, niche-differentiated and perhaps partly competitive species populations (Whittaker, 1970), thus integrating Gleason's individualistic view with the organismic approach.

Thirdly, the recognition of distinct, relatively uniform stands of vegetation may presuppose the existence of floristic discontinuities in the field. However, it is obvious that boundaries between phytocoenoses are usually not sharp, and in some cases even quite vague. Such extended boundaries are in fact concentrations of numerous small-scale subboundaries (van Leeuwen, 1966; van der Maarel, 1976). Especially those are problematic in syntaxonomy because their existence makes the localization of phytocoenoses and their classification with character species combinations a difficult procedure.

The problem of subdividing vegetation in space as well as in time is essentially a problem of scale and detail. Scale can be defined as the basic unit of surface from which data are obtained. Detail then is considered the degree to which observations and data are discriminating. Examples are the combined cover-abundance estimate of Braun-Blanquet and the criteria used for the distinction of character-taxa, companions and accidental taxa Roughly speaking, going from a very small scale to a large one, interactions between species (individuals or populations) decrease, and the differentiating effect of environmental factors increases. Phytocoenoses, as defined, usually comprise many individuals or ramets of various populations, and therefore change by the influence of environmenta factors rather than by the interaction between species. Only in their early-successional stage species interactions may predominate.

For classification purposes the description o vegetation is based on the minimal area concept o relatively uniform stands. This concept is defined a a representative area, e.g. as an adequate sample fo all species of regular occurrence (Westhoff & van der Maarel, 1973). Minimal area depends on the number of species, the size of individual plants and their clustering, and range from a few dm^2 for certain epiphytic communities to one hectare or mor for tropical rain forests. There was much debat about the reality of the minimal area in the field. A distinction between qualitative and quantitativ minimal area was suggested by Meijer Drees (1954 for forestry purposes and taken over by Beeftin (1965). In a review of current methods for minima area determination Dietvorst *et al.* (1982) starte with a systematic treatment of the relation betwee both types of minimal area and structural parameters. He then defined the analytical minimal area a the largest of the two values, because in this wa both the species richness and the dominance relations will be represented.

Recently, however, Barkman (1984) conclude that the minimal area does not exist because as a result of structure and pattern no absolute maximum in species number is reached. On functional grounds he distinguished three types of biological minimal area: (1) the minimal space area on which all species of a phytocoenose occur together in a certain developmental stage; (2) the minimal resistance area, large enough to resist disturbing influences from outside; and (3) the minimal regeneration area, which is required for maintaining the species populations in their reproduction capacity, survival in safe sites, etc. Van Delden (1984) added to the latter type the demand of maintaining a sufficient genetic variation in populations. According to him genetic impoverishment can perhaps be an independent factor in the decrease and ultimate local extinction of a population. Gene flow from other areas, such as transport of pollen and diaspores by the tides, can compensate decrease in the genetic variation of salt-marsh vegetation. Because an ecosystem may exist of species populations living together through co-evolution, the (local) elimination of one or few species sensitive to loss of genetic variation, can have great consequences for the survival of that ecosystem as a whole (van Delden, 1984). These extensions of the classical minimal area concept widen the vision of functioning in space and time of biotic elements in phytosociology, and require the solution of many problems on the level of population biology and even (eco)physiology.

The problem of scale is equally important in studying succession. Recent permanent plot studies on embanked tidal flats (van Noordwijk-Puijk *et al.*, 1979; Hogeweg *et al.*, 1985) reveal that the size of quadrats determines the result obtained as to vegetation development. Judged from small quadrats (25 × 25 cm) the vegetation tended to diverge in the course of three years. On larger quadrats (2 × 2 m) the vegetation tended to converge. Scale, therefore, has to be introduced as a variable as such in succession studies. The detailedness of observations has to be revised as well. For instance, the combined cover-abundance estimate has been found to be generally unsuitable for changes on the salt marsh (Beeftink, 1975). Estimates in percentage cover or, better in numbers of individuals and ramets in plots of the same size are preferable. In this way combined grid analyses at different scales, and numerical processing of data would make progress in studying spatial and temporal discontinuities needed of finding new conceptual traits for the different 'syn'-approaches in vegetation study.

Summarizing, the introduction of minimal resistance area and minimal regeneration area, combined with the modern view of the phytocoenose as an ensemble of species populations, will encourage integrated studies in phytosociology, population biology and ecophysiology. At present, however, a tendency towards a more reductionistic research prevails. Asking for the significance of ecophysiological and population biological results for vegetation science requires geobotanical hypotheses more adjusted to interrelationships between the different levels of biological organisation. Some problems in this field will be treated here.

Vegetation structure (synmorphology)

The structure of the salt-marsh vegetation has characteristic features. At a global scale it is related to the distribution of life forms and species (Table 1). In arctic and temperate zones the dominant life-form in the salt marsh is 'fundamentally hemi-

Table 1. Raunkiaerian life-form spectra (percentages of species number) of salt marsh and salt desert formations. T = therophytes, H = hemicryptophytes, Ch = chamaephytes, Ph = phanerophytes, G = geophytes, HH = Helo- and hydrophytes, and E = epiphytes.

Region Reference	New Zealand Chapman, 1960	New England Chapman, 1960	Great Britain Packham & Liddle, 1970	Central Europe Wendelberger, 1950	Israel Waisel, 1972	West Pacific Islands Hosokawa, 1967
T	16	15	11	34	19	–
H	56	60	55	41	35	–
Ch	4	4	8	8	29	–
Ph	8	3	5	1	17	38
G	8	11	5	11	–	–
HH	8	7	16	5	–	3
E	–	–	–	–	–	59

cryptophytic' (Chapman, 1960). In the mediterranean regions the share of chamaephytes and phanerophytes increases, and in the tropics phanerophytes, together with lianic forms, govern the structure of the mangrove vegetation. From the arctic to the tropic zones the majority of hibernating buds shifts from the soil surface or even beneath (in case of geophytes) towards levels more above the surface of the marsh.

Raunkiaerian life-forms may be considered biotic expressions of adaptation to the physical nature of the environment, such as low temperatures, ice drift, action of waves and currents. Studies on the effectiveness of these life-forms could give information on the functional backgrounds of morphological structures and physiological processes in the salt marsh. Especially species expressing themselves in more than one life-form are interesting. *Aster tripolium* is such a plastic species, showing a tendency to perenniality in the lower marsh, while annual plants occur more frequently in the upper marsh (Gray, 1971; Huiskes *et al.*, 1985).

Regionally, salt-marsh associations have characteristic differences in their life-form spectra as shown by Westhoff (unpubl.) for the Dutch Frisian Islands (Table 2). Chamaephytes are presented most in the *Artemisietum maritimae* (including *Halimione portulacoides* communities), and therophytes in the *Saginetum maritimae* and the *Puccinellietum distantis*. The latter two associations are considered characteristic for ecotone conditions (Westhoff & den Held, 1969).

Constraints in distribution are usually indicated as thermal (not traversing an isotherm) or, more general, as climatic (for instance in terms of the degree of oceanity: Jäger, 1968), or as a consequence of isolation (sea or land barriers of dispersal). The recent northward extension of the distribution areas of for instance *Suaeda maritima* and *Atriplex littoralis* in northern Norway (Skogen, 1969), *Spergularia media* on the southern Lofoten (Moe, 1970), *Carex extensa* in southern Norway (Høeg & Lid, 1949; Rørslett, 1966), and *Halimione portulacoides* and *Elytrigia pungens* on the Danish west coast (Iversen 1952–53; Beeftink, 1959) may be explained by a recent increase of seawater temperature of the west and north Scandinavian coasts. As a consequence the vegetation structure in the Skallingen salt marsh has changed considerably.

Table 2. Life-form spectra (percentage cover-abundance) of salt marsh communities from the Dutch Wadden Islands. After Westhoff (unpublished data). For the life-form symbols see Table 1.

Association	Life-forms Ch	H	G	T
Puccinellietum maritimae	6	53	12	29
Artemisietum maritimae	18	64	8	10
Armerieto-Festucetum	7	61	19	13
Junco-Caricetum extensae				
pholiurietosum	-	61	11	28
blysmetosum	6	49	35	10
Saginetum maritimae	7	44	5	44
Puccinellietum distantis	-	56	3	41

Ecological, let alone physiological explanations of distributional constraints are very rare. Crawford & Palin (1981) found that the overwintering roots of the northern coastal *Lingusticum scoticum* and *Mertensia maritima* have higher respiration rates than those of the southern species *Crithmum maritimum* and *Limonium binervosum*. They supposed that the inability to conserve overwintering carbohydrate supplies at higher temperatures is a reason for the geographic limitation in the southern distribution of these northern species.

Inversion phenomena in the zonation are another characteristic feature of the salt marsh formation. Along the European coast north of Normandy the *Puccinellietum maritimae* precedes the *Halimionetum portulacoidis* in the zonation (Beeftink, 1965). From that point southward, however, the *Halimionetum* is generally found on lower levels sometimes even growing as a pioneer vegetation on the mud (*Bostrychio–Halimionetum portulacoidis* sensu Géhu, 1975).

The reason for this inversion is not quite clear. It may be a consequence of the large tidal differences (more than 8 m) in the south draining the marsh banks more than under conditions of smaller tidal differences, and enabling *Halimione* to establish in lower zones (Beeftink, 1965). The more oceanic conditions and, in general, the higher temperatures in the south, enabling the species to grow unde more exposed conditions, are a better explanation. Such shifts to pioneer habitats is also common o foredunes, where species like *Honckenya peploides, Eryngium maritimum, Euphorbia paralias, Lathyrus maritimus* are more restricted to fore dunes and even the strandline in southern parts o their range (Doing, 1984). Apparently, a limitin factor governing in northern regions, is removed, o

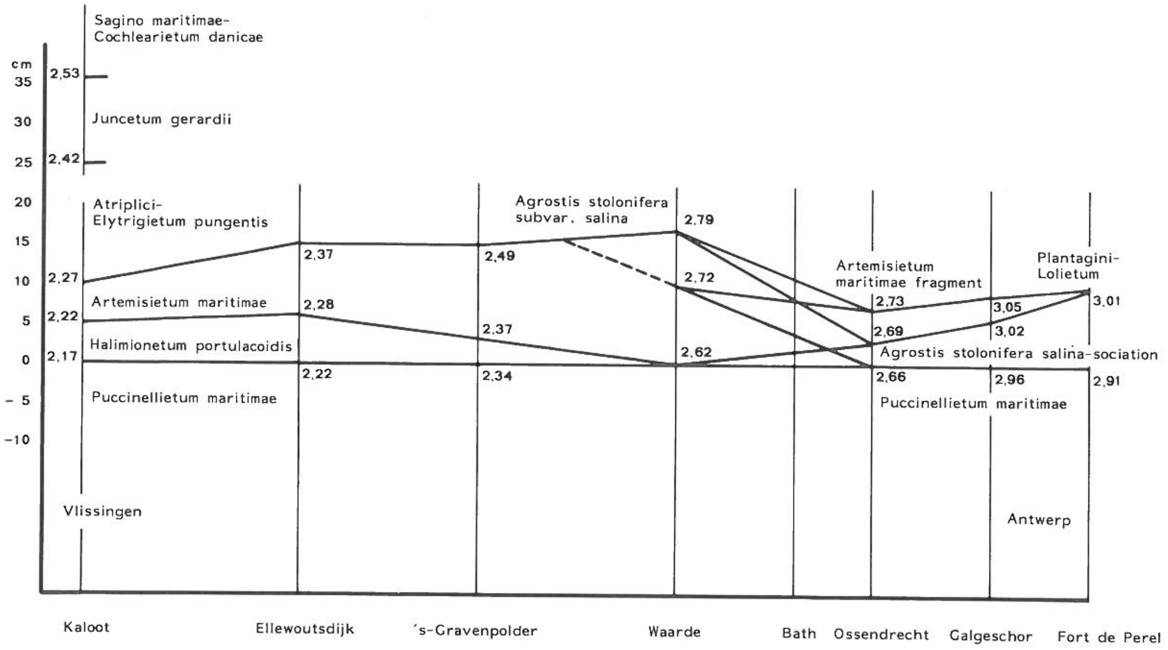

Fig. 1. Zonation of salt-marsh communities along the estuary of the river Scheldt. Each boundary line is indicated by its average level ($n = 10$–20) above NAP (Dutch Ordnance Level). Ordinate: level with respect to the average upper limit of the *Puccinellietum maritimae*. Abscis: Salt marshes from Vlissingen at the mouth (left) to Antwerp (right). After Beeftink (1965).

genetic plasticity within the species is expressed geographically.

Similar inversion phenomena exist in estuaries (Fig. 1) and in the transition zone between the North Sea and the Baltic. There, many species, such as *Glaux maritima, Juncus gerardii, Agrostis stolonifera, Puccinellia distans, Spergularia marina,* and *Atriplex hastata*, show the so-called 'diver effect' (Zonneveld, 1960). That is: under conditions of lower salinities of soil and flooding water these species are found in lower parts of the marsh enduring a higher frequency of submergence (Gillham, 1957; Beeftink, 1965). In these species flood tolerance increases with decreasing salinity. Rozema (1978) found that on a sandy and brackish beach plain species survived in zones with a lower limit depending on the degree of salt resistance, and an upper limit primarily depending on the degree of drought resistance. Flooding as such would be of minor importance as this occurs only in winter when metabolic activity is low.

On the community level, the structural architecture is the resultant of species composition, species diversity, density and the production and decomposition of biomass. Most salt-marsh species are highly light-demanding (Waisel, 1972) and under a closed canopy light can be limiting for survival of seedlings and juveniles, so that mortality is high as in the case of *Salicornia* (Beeftink, 1984).

Since the 1950's the structure of vegetation has become ever more interesting to vegetation scientists working with the Braun-Blanquet method (Westhoff, 1967; Werger & Sprangers, 1982). This led to studies on vegetation architecture, e.g. Fliervoet & Werger (1984). For the salt-marsh vegetation Buth (1984a, b) combined those studies with measurements of production and decomposition of biomass. Dynamics in the canopy structure as a result of both these processes may be decisive for changes in the species composition of phytocoenoses. His studies stress the relatively high decomposition rate of most plant materials and the role of faunal elements in this process as a functional part in the salt-marsh ecosystem.

A major question in the study of vegetation structure concerns the mechanisms causing plant communities to be floristically and structurally recognizable over geographically large areas (Beeftink, 1977a). From a population-biological and ecophysiological point of view the repeated co-occurrence of certain plant species can be explained as mechanisms of avoiding competition (Braakhekke, 1980); both spatial and functional. Spatial differentiation, or habitat differentiation sensu Braakhekke, would ultimately result in a population assemblage consisting of a mosaic of mutually independent monostands, corresponding to the heterogeneity of the environment. In this view the concept of phytocoenosis becomes questionable.

In case of functional differentiation, or niche differentiation *sensu* Braakhekke, populations of different species can live together in joint stands. Differences in species properties cause species to avoid competition for space, light, nutrients, etc. Consequently, those species can co-exist within a homogeneous environment. Such a community is in internal balance, contrary to the former which is at most an equilibrium of a mutually independent population assemblage. Because as soon as one of the populations has an ecological advantage over others such an equilibrium is thrown off its balance.

Three remarks follow from these theoretical considerations.

(1) Not a single environment or habitat can be considered totally homogeneous, nor extremely heterogeneous. Hence the populations of plant species living together in a phytocoenose could be considered as the expression of an assemblage or pattern of so many microhabitats. But both in population and habitat assemblages the problem of scale arises: at what size can microhabitat assemblages be considered a matter of within-diversity, and at what size that of between-diversity? Here, again, the minimal area concept must be introduced.

(2) 'Considering' is a major characteristic feature of a paradigmatic view. The problem remains how to break open the paradigms of holism (functional differentiation) and reductionism (spatial differentiation). After Sloep (1983) this could be elaborated by erecting a system of axioms co-ordinating basic concepts, such as spot, environment, niche and species. Such axioms could then be formulated both in vernacular and formal languages enabling geobotanists to process them further in these two ways of conceptualism.

(3) (Semi)natural population assemblages have their own historical roots. Some populations may be in fact the remnants of former communities, others are representants of the present, or even the precursors of a future community. The question is how all these populations forming an assemblage are equal partners in a phytocoenose, and how they can contribute to a characterization of related phytocoenoses for a classificatory system. A. Beeftink (1984) tackled this problem for *Limonium vulgare* and *Plantago maritima* growing together in the *Plantagini–Limonietum*.

Succession (syndynamics)

On the salt marsh one or a few species are usually dominating in a phytocoenose. Mosaic structures are only common in some types or developmental stages of the *Puccinellietum maritimae* and in some *Armerion* communities. Grazing promotes the development of multispecific stands (Bakker, 1984). This could mean that in the absence of large herbivores succession has generally a rather rigid or obligatory character (Horn, 1976). It is not yet known how the models of Connell & Slatyer (1977) relate to succession on the salt marsh. However, because early successional stages are predominantly determined by abiotic factors (Beeftink, 1977a), the facilitation and tolerance models may both be applicable.

The introduction of *Spartina anglica* to large coastal areas has caused a great disturbance in the original successional trends. This species is the most recent example of (semi)spontaneous polyploidy in the salt marsh, and is also one of the few taxa with a C_4-photosynthesis. About 120 years ago it has been introduced as a hybrid of the North American *Spartina alterniflora* and the European *S. maritima*, in which soon doubling of the chromosome number occurred. The ecology of this amphipolyploid corresponds to the inhibition model of Connell & Slatyer (1977): in old *Spartina* fields, especially those grown up from bare mud, die-back phenomena occur before the vegetation is being succeeded by species of other successional stages (Goodman *et al.*, 1959, 1961; Goodman, 1960). Beeftink (1977b) suggested that soils with *Spartina anglica* generally develop to a more waterlogged state, so that they become less suitable for subsequent recruitment of both early and late successional species. *Spartina* promotes sedimentation of

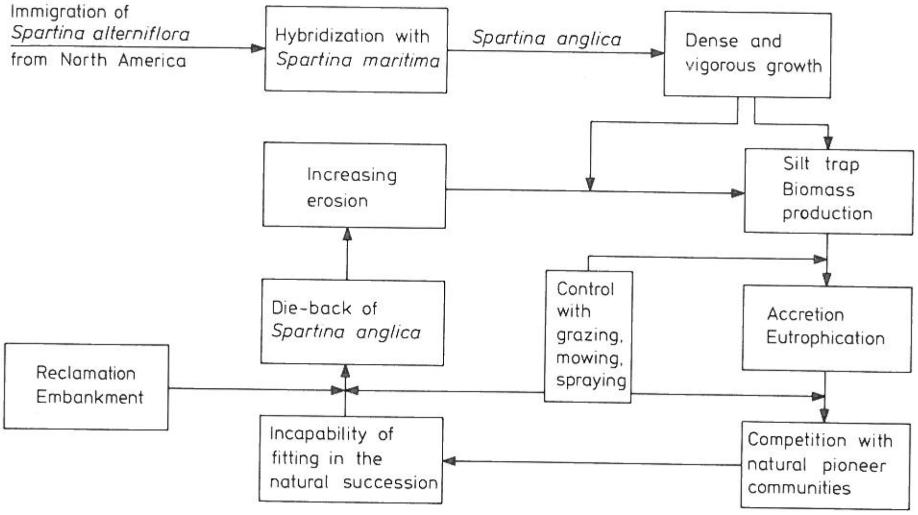

Fig. 2. Disfunction of *Spartina anglica* after invading the salt-marsh ecosystem. After Beeftink (1975a), with permission of the British Ecological Society.

silt, and enlarges the content of organic matter in the soil promoting the development of toxic reduced S compounds. Its dense growth and high biomass production also impedes the penetration of light necessary for the establishment of the mostly high light-demanding plant species. Therefore, only large invaders, such as *Scirpus maritimus* and *Phragmites australis* occurring in brackish marshes can eliminate *Spartina*. In saline environments, however, *Spartina* communities would persist until they are damaged, either by waterlogged soil conditions, or by parasites (the aphid *Sipha littoralis* (Walker) for instance), or by grazing (Fig. 2). Grazing is one of the few factors suppressing *Spartina*, and enabling the establishment of other species in substantial numbers.

Succession is a very complex process, even in the salt marsh. Its understanding needs a careful analysis of vegetation dynamics and their environmental relations (compare Roozen & Westhoff, 1984; A. Beeftink, 1984).

Flooding frequencies may vary considerably from year to year as a result of differences in wind action and of the 18.6-yr cycles turning of the moon's orbit plane. These variations can be characterized by totalizing the deviations (in cm) of the actual high water level (monthly averages were used here) from mean high water level (1951–60, corrected for the influence of the moon's orbit plane) over a series of vegetation periods (Table 3). These periods were chosen as intervals between the months in which successive yearly relevés of permanent plots have been made (September–August). In this way the period 1962–65 can be characterized as having a relatively low tidal influence. The periods 1965–70 and 1957–62, on the contrary, showed a higher tidal influence compared with mean figures.

A low tidal influence will initiate physical and chemical soil-ripening processes, such as desiccation of the upper soil layers, oxidation of metal and sulphur compounds, and perhaps desalinization. High tidal influences on the salt marsh will promote the reverse. It may therefore be supposed that low tidal influences promote succession processes in the vegetation, while high tidal influences give a start to regression phenomena.

This is illustrated in Table 3: changes in cover percentages of plant populations on permanent plots coincide to a high degree with variations in tidal difference, especially where a period of higher flooding frequencies than 'normal' passed into one with less (1962–1963) and reverse (1966–1967). Moreover, the data from the four permanent plots in Table 3 show that the character of the change in cover percentage of a plant population may depend on the level at which the plots are lying in the marsh. *Aster tripolium*, for instance, has higher densities in the two lower permanent plots, but lower densities in the two higher plots during the period of low tidal influence. Apparently, the *Aster* population is shifting over the marsh dependent on the impact of the tides. A similar reaction is found in *Halimione portulacoides*.

Suaeda maritima and *Salicornia europaea* are increasing their populations considerably over large parts of the salt marsh because seed dispersal is promoted under the influence of tidal currents (see also Beeftink, 1984). An increase in population density under such conditions, but then partly also on the strength of vegetative growth, is also found among *Spartina anglica, Triglochin maritima* and *Limonium vulgare*. *Elytrigia pungens, Festuca ru-*

Table 3. Estimated cover percentages of plant populations and numbers of molluscs over 1962–70 in four permanent plots laid out in the Springersgors salt marsh, Grevelingen. Deviations (cm) of actual high water level (monthly avs.) from the corresponding mean high water level (1951–60) of the Vlissingen tide-gauge station. Symbols for mollusc densities: r = rare, o = occasional, f = frequent, and a = abundant. Height of the plots 1.41, 1.49, 1.54 and 1.70 m + NAP (Dutch Ordnance Level) respectively. Mean high water at Springersgors salt marsh 1.28 m + NAP.

Sample plot No. 1

Year	62	63	64	65	66	67	68	69	70
Deviation of HWs from MHW in preceding period (accumulated)	+97	-52	-29	-3	+60	+48	+21	+12	+34
Puccinellia maritima	80	80	90	80	90	60	10	15	10
Aster tripolium	2	5	10	4	4	2	2	1	1
Glaux maritima	–	–	1	2	2	–	–	–	–
Plantago maritima	–	1	1	1	1	1	–	–	–
Limonium vulgare	10	20	30	20	20	20	30	20	20
Suaeda maritima	3	3	2	3	2	3	3	3	10
Halimione portulacoides	3	3	3	3	2	1	3	–	1
Spartina anglica	2	2	2	1	1	1	2	3	2
Salicornia europaea	5	3	2	3	4	30	30	15	20
Triglochin maritima	–	1	2	3	3	10	20	15	10
Hydrobia ulvae	f	o	o	o	r	r	a	f	–

Sample plot No. 2

Year	62	63	64	65	66	67	68	69	70
Deviation of HWs from MHW in preceding period (accumulated)	+97	-52	-29	-3	+60	+48	+21	+12	+34
Festuca rubra	3	5	10	10	10	2	2	3	
Elytrigia pungens	–	–	–	1	1	–	–	–	
Artemisia maritima	–	2	2	2	2	3	1	–	
Parapholis strigosa	2	–	–	–	–	–	–	–	
Plantago maritima	5	15	10	10	10	10	10	10	
Aster tripolium	3	15	10	30	20	4	4	20	
Glaux maritima	10	10	10	10	10	4	4	4	
Halimione portulacoides	30	25	30	20	10	10	4	4	
Salicornia europaea	4	3	–	1	4	20	10	5	
Suaeda maritima	4	3	–	3	5	20	15	4	
Puccinellia maritima	1	–	1	–	1	1	2	2	
Spartina anglica	–	–	–	–	–	1	1	2	
Limonium vulgare	50	40	40	30	50	60	70	70	
Triglochin maritima	2	1	1	2	3	2	3	2	
Spergularia media	2	3	3	1	2	2	2	2	
Littorina saxatilis	–	–	–	r	r	r	f	f	
Assiminea grayana	o	–	o	–	r	–	o	f	
Ovatella myosotis	o	–	–	–	–	–	–	–	

Table 3. Continued.

Sample plot No. 3

Year	62	63	64	65	66	67	68	69	70
Deviation of HWs from MHW in preceding period (accumulated)	+97	-52	-29	-3	+60	+48	+21	+12	+34
Elytrigia pungens	100	100	100	100	100	70	80	70	
Halimione portulacoides	30	2	1	–	2	2	10	10	
Aster tripolium	10	3	3	–	2	4	5	10	
Suaeda maritima	4	–	2	1	20	45	20	30	
Artemisia maritima	2	1	1	–	1	1	–	–	
Limonium vulgare	–	–	–	–	–	1	–	–	
Salicornia europaea	–	–	–	–	–	–	–	1	
Assiminea grayana	o	o	f	a	r	–	–	–	
Ovatella myosotis	a	o	o	o	a	a	a	o	

Sample plot No. 4

Year	62	63	64	65	66	67	68	69	70
Deviation of HWs from MHW in preceding period (accumulated)	+97	-52	-29	-3	+60	+48	+21	+12	+34
Elytrigia pungens	5	30	40	60	70	70	30	50	
Festuca rubra	70	80	100	90	80	40	55	60	
Artemisia maritima	40	30	20	10	10	4	3	3	
Salicornia europaea	–	–	–	–	–	2	4	1	
Suaeda maritima	2	–	–	–	–	10	30	3	
Aster tripolium	3	2	1	2	1	4	4	4	
Puccinellia maritima	2	–	–	–	–	–	–	–	
Spergularia media	1	–	–	–	–	–	–	–	
Plantago maritima	4	3	2	3	2	2	2	1	
Limonium vulgare	2	1	2	1	1	1	1	1	
Halimione portulacoides	3	2	1	2	2	3	3	2	
Assiminea grayana	f	–	–	–	r	o	–	o	
Ovatella myosotis	o	–	–	–	f	f	a	o	

bra, *Artemisia maritima* and *Glaux maritima* appear sensitive to tidal immersions of seawater. Also the salt marsh molluscs appear to react upon tidal impact in their densities. The inundation experiments carried out by Groenendijk (1983, 1984) for some of these plant species showed similar results, but revealed that temperature and developmental stage of the plants are important variables for fitness after the impact of inundation.

The cover percentages of the plant populations also suggest that they do not return to the former situation after an interval of low tidal influence. In sample plot No. 1, for instance, *Triglochin* seems to establish itself firmly under high tidal impact, while *Limonium* does not yield ground, in this plot, as well as *Plantago maritima* in plot No. 2. *Artemisia*, however, does not make use of the space left by *Elytrigia* for recovering itself, in 1967–69. The conclusion is that years with much wind action on the flood level, especially by lowering the high-water level, and perhaps also the 18.6-yr cycle of the turning of the moon's orbit plane, may stimulate succession. Among the other environmental factors involved in this process the sedimentation rate takes an important part. Net accretion (shrinking included) of the salt marsh soil may vary considerably from place to place, for instance from 1.6 to 11.6 mm/yr over 19 years (1965–84) in an Oosterschelde salt marsh (Beeftink, unpubl.). In other areas such as on the borders of the Westerschelde, accretion

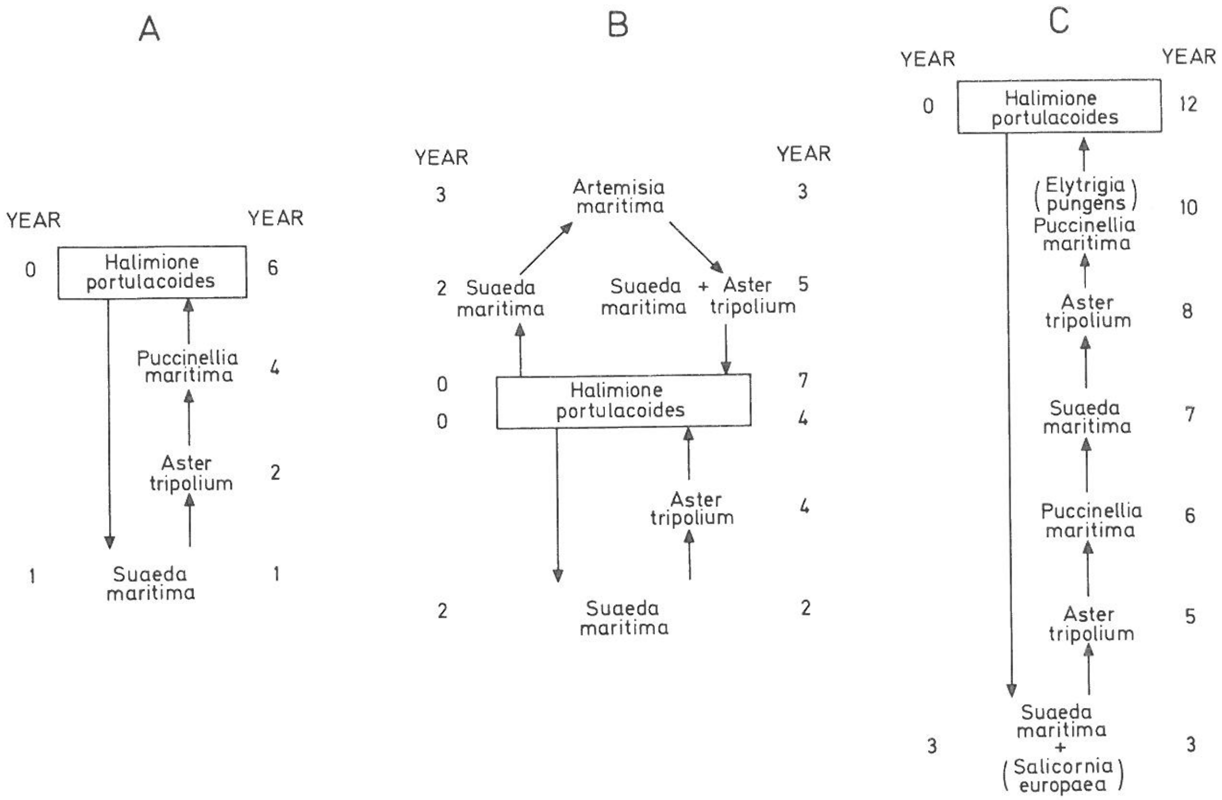

Fig. 3. Models of plant succession after three types of environmental disturbance in *Halimione portulacoides* communities. A. After waterlogged conditions. B. After severe winter frost. C. After chemical destruction. The numbers following arrows indicate the years in which maximal population densities of species were observed after the year of disturbance (year zero). After Beeftink *et al.* (1978a).

can be expected as a result of human interference (dredging) with estuarine hydrology, so that this factor in its turn can interfere with climatic and planetary influences to a great extent.

A second group of environmental impacts on the salt-marsh vegetation is formed by natural disturbances. They are mainly initiated by exceptional climatic influences: periods of extreme coldness such as in the 1961–62 winter, long periods of rainfall resulting in waterlogged or even immerged conditions, very hot and dry periods raising soil salinity to extremely high values. All these types of disturbance may result in die-back phenomena in plant populations, sensitive to those conditions, leaving patches of bare soil on which a secondary succession will run (Fig. 3). From such succession series examined in permanent plots laid out in different salt-marsh communities a scheme was developed showing (a) that distinct species (mainly *Salicornia, Suaeda, Aster, Puccinellia maritima* and *Glaux*) are acting in secondary succession, and (b) that secondary succession is becoming more complex running from the pioneer communities on the mud flats, over the *Puccinellion* communities in the middle salt marsh to the *Armerion* communities in the upper marsh (Fig. 4). These gap fillers are distinct in their ecology from other salt-marsh species (left in Fig. 4) which seem to be especially sensitive to the impact of the tides and sedimentation.

The last point in this study on vegetation dynamics deals with ancient human interferences for agricultural and civil-technical purposes (see also Beeftink *et al.*, 1978b). These effects are illustrated, as an example, with an experiment started 1971 in a *Puccinellietum maritimae* community. The treatments were (A) control (only slightly trampled), (B) mowing and removing the cut grass each year, (C) covering with a soil layer of 10–15 cm after mowing the sward in winter 1971–72, (D) cutting sods, and (E) excavating 25 cm in winter 1971–72. Table 4

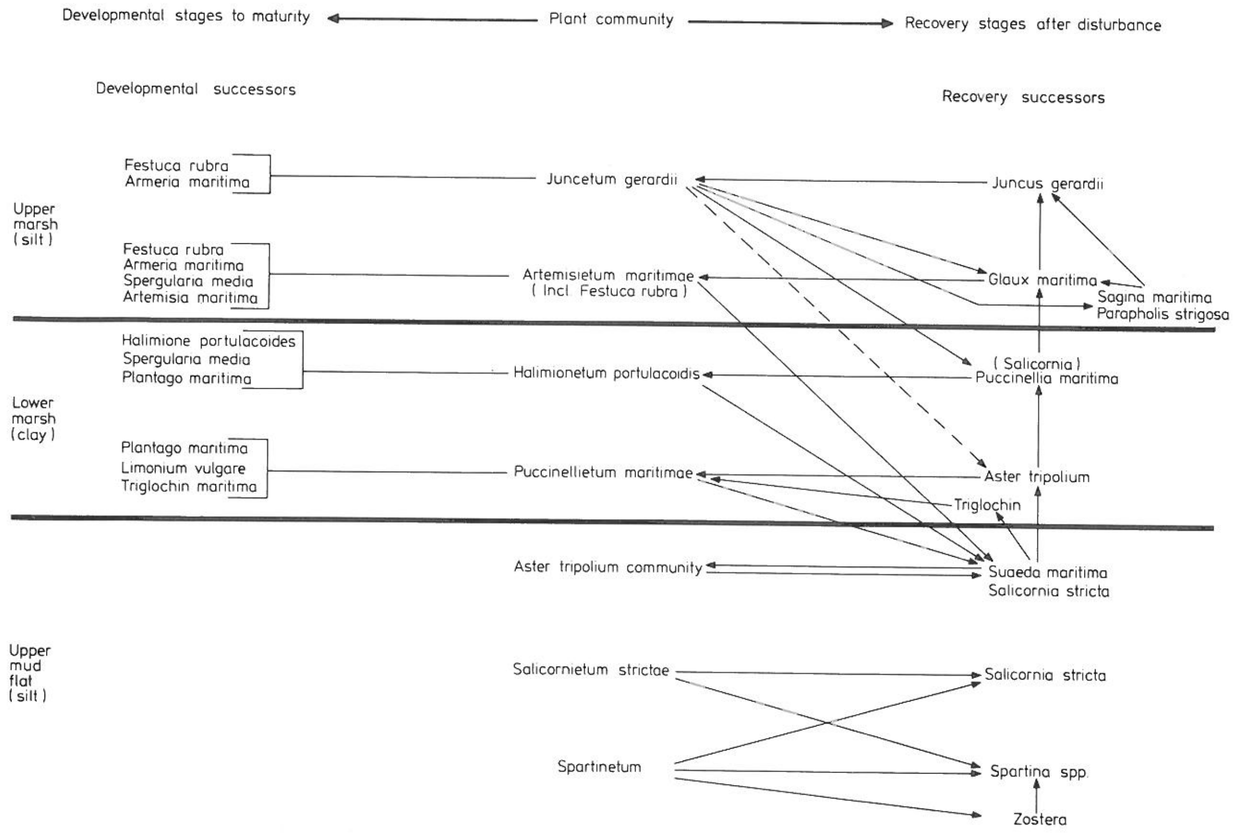

Fig. 4. Interrelationships between plant populations and communities in the salt-marsh ecosystem in relation to environmental disturbances. The arrows indicate sequences of developmental stages in secondary succession after disturbance. The species at the left side did not react on the types of disturbance examined. After Beeftink (1979) reproduced by permission of Blackwell.

Table 4. Cover/abundance estimates (August 1971) according to Doing Kraft (1954) on the plant species growing in the experimental plots before interferences with management measures. Location: Stroodorpepolder salt marsh (Oosterschelde). A = control, B = mowing, C = soil supply, D = cutting sods, E = excavation (compare Fig. 5). Start of the experiment winter 1971-72.

Cover	A	B	C	D	E
Puccinellia maritima	07	07	07	07	04
Limonium vulgare	04	03	03	04	05
Triglochin maritima	m	01	01	m	m-01
Salicornia europaea	m	m	m	m-01	m
Suaeda maritima	m	m-01	m-01	m	m
Aster tripolium	m	a	m	a	m-01
Halimione portulacoides	a	a	p-a	a	a
Spartina anglica	a	a	p	a	p
Spergularia media	p	r	r	–	p
Plantago maritima	–	r	r	p	a
Armeria maritima	–	–	–	–	r

shows the floristic composition of the plots before starting the experiment. The vegetation varied only slightly. Only plot E (excavating) deviated somewhat owing to a slightly higher position (some cm) with respect to the other plots. In Figure 5 the impact of the four management measures are depicted. Only those species are included in the graphs which showed evident effects.

The control plot (Fig. 5a) showed an antagonistic behaviour of *Puccinellia* and *Triglochin*, comparable with the behaviour of these species in plot No. 1 in Table 3 and probably also caused by tidal variations. *Suaeda* followed roughly *Triglochin* in its cover/abundance fluctuation; *Halimione* faded away. Mowing (Fig. 5b) resulted in an evident increase of *Triglochin*, ultimately at the cost of *Puccinellia, Limonium* and *Spartina*. Supply of soil (Fig. 5c) gave rise to a subsequent increase and fall

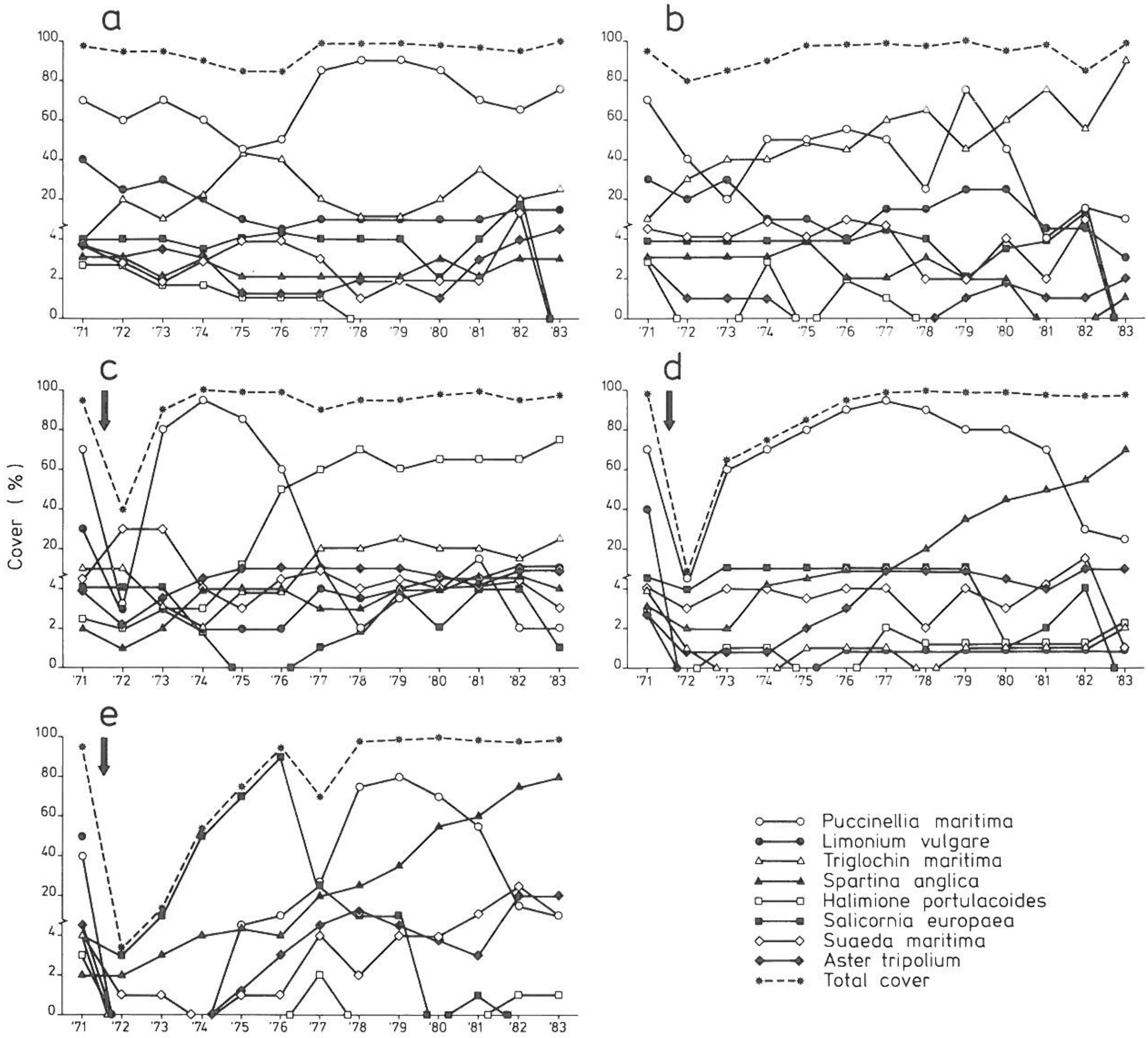

Fig. 5. Effects of human interferences for agricultural or civiltechnical purposes in the salt marsh examplified for a *Puccinellietum maritimae* community of the Stroodorpepolder salt marsh (Oosterschelde). Treatments: A. Control (only slightly trampled). B. mowing and removing the cut grass each year. C. Covering with a soil layer of 10–15 cm after mowing the sward. d. Cutting sods, and E. Excavating 25 cm. Start of the experiment winter 1971–72.

of *Suaeda* and *Puccinellia*, followed by a longer lasting increase of *Halimione* changing the vegetation towards a *Halimionetum portulacoidis* phytocoenose. The high densities of *Puccinellia* in 1973–76 caused a temporal decrease in *Triglochin, Suaeda* and *Salicornia*. *Limonium* suffered from soil supply as such, just like *Puccinellia* and *Suaeda* in the first year after soil supply. *Spartina* slightly increased and maintained.

Cutting sods (Fig. 5d) which in fact means the removal of hibernating buds, seed banks and nutrients and an increase in the frequency of flooding promoted the extension of *Puccinellia* heavily, and, in a slower pace, that of *Spartina*. *Limonium* and *Triglochin* had no chance for recovering, contrary to *Suaeda* which maintained at higher densities after an initial fall. Excavating (Fig. 5e) had a more violent impact giving a sharp rise and fall in density to *Salicornia, Aster* and *Puccinellia* successively. These fluctuations went together with a steady increase of *Spartina* changing the vegetation more emphatically towards a *Spartinetum* community than in the case of cutting sods.

All these environmental relations clarify successional trends in the salt marsh so far that they stress the local hydrological conditions as a paramount factor. Lowering the soil surface by excavating, or sheet erosion, and raising it by soil supply, or sedimentation, give rise to regression resp. succession. But also changes in the tidal factor show similar shifts in the vegetation composition. A second point is that each species appears to have its own characteristic response on these hydrological conditions interfering on the population level. This is reflected in different aspects of the life cycle: the hydrochoric dispersal of seeds, such as in *Salicornia, Suaeda, Atriplex* and *Aster* (Beeftink, 1985; Huiskes *et al.*, 1985), the effect of wave action on the seedlings and juvenile plants, such as in *Salicornia, Suaeda, Spartina* and *Aster* (Groenendijk, 1985; van Eerdt, 1985), germination in relatin to deposition of sand and silt, illustrated by A. Beeftink (1985) in *Plantago* and *Limonium*, and the sensitivity to toxifying agents and nutrient availability in relation to the redox potential of the soil found in different species (Groenendijk, 1985; Havill *et al.*, 1985; Rozema *et al.*, 1985; Singer & Havill, 1985).

Besides the tidal factor, natural climatic disturbances in the vegetation canopy induce patch-like secondary succession series (Beeftink *et al.*, 1978a, Beeftink, 1979), and man and large herbivores modify the structure and composition of vegetation at different scales by their management measures and varied grazing pressure (Bakker *et al.*, 1983; Bakker, 1985; Vestergaard, 1985). All these environmental disturbances and processes can stimulate the generation turnover, or at least influence age distribution spectra in perennial species. An intriguing problem to solve is how these reactions are among the species and types of environmental change, and what their impact is on gene flow and genetic variability in relation to the maintenance of populations (cf. Gray, 1984). This all makes spatial and temporal relations in the salt marsh very complex, even though only few species of higher plants are involved in this ecosystem.

History of salt-marsh vegetation (synchronology)

Since postglacial times salt-marsh vegetation does not seem to have changed substantially in floristic composition. Pollen and seed records produced by Bakker & van Smeerdijk (1982) from the Ilperveld suggest a vegetation pattern before about 4600 BP comparable with that in roman times. And Behre (1976) reported that salt-marsh communities which occurred around (post)Roman settlements in NW Germany probably did not differ from present-day communities. However, changes in salt-marsh development are evident through (pre)historic times. Pethick (1980) pointed out that in North Norfolk salt marshes a coincidence exists between marsh inception and a moderate sea level rise, suggesting that salt-marsh development occurred parallel to the successive periods of sea level rise.

This brings us to the question how temperate coastal halophyte vegetation survived glacial times. It is well known that such vegetation needs marine supralittoral silt deposits. Saline marsh formations develop mainly in the neighbourhood of rivers as estuarine and deltaic deposits built up under the influence of fluvial silt discharge. More rarely, they can be formed in coastal bays as a result of reworked materials originated from eroding clay banks and other ancient deposits in front of the coastline. Wolff (1972) argued that during the last glaciation all present-day rivers of NW Europe were tributaries of one enormous stream discharging itself in the Atlantic Ocean somewhere to the west of the present-day entrance of the English Channel. Similar estuarine areas were found in the Loire and the Garonne-Gironde system. The nearest river mouths to the south were at the west coast of the Iberian Peninsula, separated from the former by ca 600 km of steep and rocky coasts. It can therefore be argued that saline marsh formations were more disjunct and more scarce in glacial times than at present.

Another feature was that during glacial times the large areas of continental platforms and the polar desert climate (van der Hammen, 1979) allow the finer moraine fractions to be transported mainly by wind. Therefore, glacial rivers discharged possibly relatively more coarse materials than rivers do under warmer and more humid conditions. For that reason it may be assumed that coastal silt

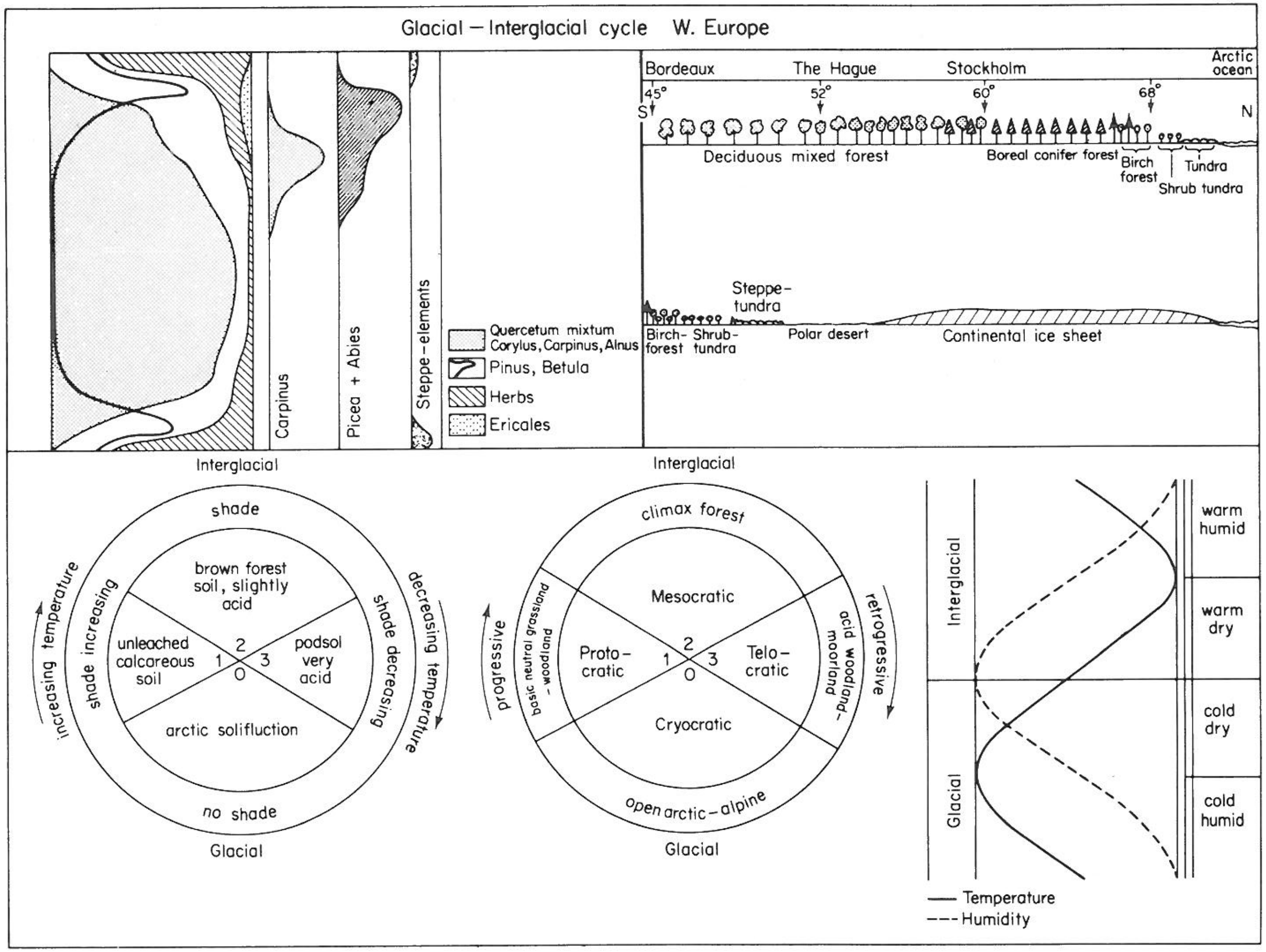

Fig. 6. Schematic representation of the glacial-interglacial cycle in NW Europe. After van der Hammen *et al.* (1971) reproduced by permission of Yale University Press.

deposits were also less extended in glacial times than in the last millennia.

Although less in number and extension those habitats could still be suitable refuge areas for temperate coastal halophytes during glacial times. Their functioning as such will depend mainly on the minimal regeneration area required for maintaining each of the species populations survived (Barkman, 1984), and on the effectiveness of the diaspores to be dispersed over long distances along the coast by sea currents or birds.

It is therefore worth examining the alternative of taking refuges in coastal sites, i.e. temperate halophyte species could also have found such areas in inland habitats. This possibility is supported by the view upon glacial life conditions put forward by van der Hammen and collaborators (van der Hammen *et al.*, 1971; van der Hammen, 1979). They argued that in interglacial periods the humid climate turned the vegetation to closed woods and the soils to increasingly acid. The cool to cold and dry glacial periods, on the contrary, promoted a regression towards open steppes and tundras, or even polar deserts, and the soils becoming increasingly alkaline, localy admitting certain saline conditions (Fig. 6). Indeed, drought and frost stresses seem to have similar effect as salinity by acting upon cellular membranes of halophytes increasing both transpiration and the accumulation of salt within cells (Vieira da Silva, 1978).

It could therefore be hypothesized that during interglacial periods – as in modern times – sea level rises, together with an enhanced sediment discharge by the rivers, promoted the development of coastal salt-marsh vegetation. In glacial periods, however, halophytes should have found refuge areas on more southerly coastal habitats and on inland alkaline soils.

Yet it remains questionable whether saline soils are adequately widespread in the interior during glacial times, either over permafrost (Monoszon, 1967; Bell, 1969) and/or by eolic salt transport from the seas (Tolstow, 1964, in Frenzel, 1968). Halophytes require more environmental conditions for survival. One of them is a high light intensity of the habitat combined with a low competition pressure from glycophytic forms. This was favoured by the open character of the glacial steppe and desert vegetation. Adam (1977) therefore stressed the importance of this factor especially with respect to the then much more widespread *Armeria maritima* and *Plantago maritima*.

Another factor governing inland halophyte distribution could be the content of boron which seems to be evidently higher in saline and related soils (Breckle, 1975). Goodman (1973) indicated boron as another factor in the surviving mechanisms required by plants in the salt desert in Utah. Those halophytes, such as *Atriplex nuttallii*, even show ecotypic differentiation with respect to both salt and boron tolerance. Scharrer & Kühn (1955) found high boron tolerances in Chenopodiaceae, and lower tolerances in Leguminosae en Gramineae. Breckle (1975) showed that inland halophyte species from Utah have significantly different optimum ranges. He hypothesized that the composition and pattern of vegetation are not only determined by the distribution of salt in the soil but also by that of boron.

These considerations suggest that a low competition level combined with low temperatures in an alkaline environment could perhaps more or less compensate the temperate salinity conditions for halophyte survival, or – as suggested by Rozema (1978): saline habitats are safe sites or refuges for halophytes because glycophytes have no or only little ecological possibilities for invading and growing in such habitats, or – in other words: halophytes do not strictly need the present-day saline habitats; under other climatic conditions they could perhaps also maintain in other habitats, either past or present, where non-halophytes have a lower relative growth rate.

Conclusion

Harper (1982) rightly stated that the phytosociologist has a geographical rather than a functional approach, and is interested in species and area rather than in individuals and pattern. This difference in attitude is beginning to fade away, but much has still to be achieved for a working integration of both geobotanical approaches. This is illustrated in a recent paper of van der Maarel (1984) who compared population biological items derived from Harper's (1977) standard work with corresponding synecological approaches. Such comparisons will help to encourage new studies where they are most needed to understand structure and functioning of existing salt marshes, but also to design new coastal environments for ensuring adequate stepping stones in these very characteristic biota.

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