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Experimental plant ecology as an approach in coastal population biology

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Abstract. The relations between a large number of scientific subdisciplines within the population biology of plants are presented.

This overview in which the holistic and reductionistic approaches are discussed, emphasizes that conflicts between both attitudes are artificially raised. In fact, the one approach must support the other in order to trace the relations between the individual plants and their environments and to understand their performance at the population or community level.

To illustrate this way of gaining insight into the richness of diversity in nature, two examples in experimental plant ecology are given.

1. Introduction

Population biology of plants, a synthetic discipline, comprises a large number of scientific fields. Geobotany, population dynamics, population genetics, physiology with adaptive morphology, demography, ecology at the population level, and experimental plant ecology are topics incorporated in the field of population biology. The ultimate constituents of the population are individual organisms that can, potentially, interbreed (Krebs 1985). Central to studies in population biology is a need to understand characteristics of individuals within populations. Furthermore, it is crucial to understand the dynamics of the communities in which those individual plants and their populations occur.

Different approaches can be applied to analyse the processes which control the structure and composition of vegetation. One of these approaches is to explain variation of vegetation by reference to associated environmental variation. To understand the processes determining characteristics such as variation within and between populations, a study of interactions between neighbouring species is indispensable. In fact, all studies aiming to explain the structure and func-

tioning of populations should begin with an accurate description of the vegetation in which the populations occur. Plant sociology is one of the possibilities in the gathering of information on the composition of plant species in communities. The concept of plant community has been reviewed by e.g. Westhoff and van der Maarel (1973). These authors indicated that the term plant community has been used in both concrete (phytocoenose) and abstract (phytocoenon, community type) senses. They present definitions in which separate descriptions of concrete and abstract communities were linked in a general definition of vegetation. Following these authors, vegetation is a system of largely spontaneously growing plant populations: growing in coherence with their abiotic environment and forming an ecosystem with all other forms of life occurring at their sites. Recently, Harper (1982) reported that plant communities can be defined, whether objectively or subjectively, as assemblages of species which are treated as objects for classification or ordination.

In my view plant sociology, in terms of recognizing groups of naturally neighbouring species, is indeed the first stage before entering studies on the population level, but an approach from the viewpoint of geobotany, a scientific field which is

aimed at ascertaining the essential features and recurrent patterns of spatial distribution of plants, is the necessary second stage in obtaining insight into the causes of why certain assemblages of species occur. The need for research into the composition of the vegetation has often been underestimated. This is also the case for studies on interactions between soil properties and species composition. Boorman (1977) stated that phytosociological research is not so easily applied and operators have to learn to recognize particular associations in the same way that a plant species is recognized. However, understanding the factors determining the variation in species composition is even more complicated. Therefore vegetation research is mostly descriptive and only correlative relations can be revealed. Nevertheless the knowledge of the structure, composition, and processes, such as succession, must be a basis for further studies, for example on the level of individual plants. When the characteristics of the separate individuals are known, the observed characteristics of higher levels of organisation, population or vegetation, can be explained to a large extent. However, many vegetation researchers will state that the characteristics of the vegetation as a whole, will be more complicated than the sum of the characteristics and interactions of all species constituting together the vegetation (e.g. Westhoff 1972). Therefore the knowledge of the separate individual plants, combined with insight into processes which take place within the vegetation, is the very best approach in ecological and population biological studies.

Population dynamics can be described as a study on changes in numbers of plants, birth and death rates, and on immigration and emigration (e.g. Harper 1977).

Population genetics includes studies on genetic differentiation in populations, natural selection, and evolution (e.g. Solbrig *et al.* 1979; Jacquard *et al.* 1985).

In a changing environment, plants will develop mechanisms to survive the new climatic and edaphic factors. Morphological changes within plants occurring in changing environments are often the results of changing physiological processes. Physiological ecology at the level of populations provides studies of the physiological processes determining sizes, birth, and death-rates

of individual plants. It is necessary to interpret plant forms in terms of function, understanding of basic phenomena such as growth, the biochemistry of photosynthesis, the mechanisms of water and nutrient transport. To understand intra- and interspecific interactions and their effects on the structures of populations, physiological studies must also be performed. Demographic techniques are used to quantify varying densities of plants in their areas of distribution in relation to different stages in the life cycle of plants. One of the main aims of demographic research is to construct life tables. A life table is a convenient format for describing the mortality rate of a population. In other words a life table is an age-specific summary of mortality rates operating on a population. Life tables can be calculated on the basis of a cross section of the population at a specific time, the static life table; or can be calculated on the basis of a cohort of organisms followed throughout life, the cohort life table. Some authors (e.g. Harper 1977) consider two principal objectives of plant demography. First, demographic studies are carried out by agriculturalists for practical purposes and second, demographic data are gathered in order to understand the dynamics of a population and the action of natural selection. In their view, the concept of natural selection is basically a demographic concept and therefore natural selection must be measured directly in natural populations. However, from studies carried out by plant geneticists, it can be stated that natural selection is the result of presumably adapted characteristics (e.g. Solbrig 1980). Measurements of demographic characteristics of plants will not be sufficient to find out the processes causing selection. In my view plant demography must not be considered as an independent scientific field; it is, in the first place, a technique in order to trace parameters such as natality, immigration and emigration in populations. The underlying causes of the values found in these parameters must be unravelled by studies, for example, on the level of population genetics or on that of population and experimental ecology.

Population ecology is primarily focussed on the relationship between given characteristics of individual plants within different populations and complexes of environmental factors. In life-history studies, life span, competition, and reproduction

must be considered in an integrated context. This will contribute to the understanding of the diversity of reproductive strategies.

Tracing causal relationships between plant characteristics and environmental factors needs an experimental approach and is the aim of experimental plant ecology. The first step in experimental plant ecology is a study of the plants in their natural habitat. A hypothesis on the main environmental factors affecting the behaviour of the plant under study must be derived in the field. Therefore demographic measurements and characterisation of environmental factors are essential. Soil and climatic characteristics have to be analysed. Variation in plant characteristics and in environmental values have to be investigated by long term observations. Under natural conditions the occurrence and performance of an individual plant reflect the effects of the interaction of many environmental factors, so the second step is to design experiments under controlled conditions in order to investigate the separate and combined effects of the observed environmental factors of the plants under study. In this manner the hypothesis is tested. The third step is the re-checking, in the field, of the results obtained in the growth-cabinet, greenhouse or in experimental plots. Another basic point in experimental plant ecology is that the effects of specific factors must be studied during all stages in the life cycle of the plants. The effects of environmental conditions may change after the germination phase or during seedling establishment, growth, flowering and reproductive stage (Blom 1978). Furthermore, questions as to how plants interact with each other (inter- and intraspecific) and with other organisms are topics involved in this field of research. The various approaches in experimental plant ecology are presented schematically in Fig. 1.

It will be clear from the above survey of the disciplines belonging to or supporting population biology that these different fields of scientific activities cannot be clearly separated. Most of these approaches interact with each other. Recently, this field of research has been mentioned as a part of the distinct subdiscipline, functional ecology (Calow 1986).

One of the aims of this overview is to emphasize that conflicts between different approaches are artificially raised. Indeed, a holistic approach

such as phytosociology differs markedly from a reductionistic attitude. However, the one approach must support the other, which is clearly illustrated in the work of Wim Beeftink. He started his career with descriptive studies of the vegetation and habitat of salt marshes and beach plains (Beeftink 1966, 1968, 1972). As with many phytosociologists, his first field of research was in the description of a nearly-undisturbed wilderness of communities and he found many correlative relations between plant composition and environment. Later on he published work on the effects of shifts in environmental conditions on species composition of coastal areas (Beeftink 1975). Subsequently he and his co-workers became more interested in aspects of population dynamics (Beeftink *et al.* 1978, Beeftink 1985a, Huiskes 1980 and Huiskes *et al.* 1985). They started to look at individual organisms, studying parts of communities, the sum of characteristics of these parts and their mutual interactions. Beeftink always stated that the vegetation is the generator for population biological and physiological studies and he illustrated that belief in his research on the salt marshes (Beeftink 1985b). That was his way of gaining insight into the richness of biotic diversity in natural communities.

In this chapter a few examples of experimental studies on the ecology of some plant species are given, but certainly not in the sense of autecology. The ultimate aim of these studies is to obtain insight into different ecological aspects of these species in order to understand the performance at the population and community level.

2. Interactions between *Glaux maritima* and *Plantago maritima*

In a field study at the nature reserve Kwade Hoek, isle of Goeree, the Netherlands, the spatial distribution of *Glaux maritima* L. and *Plantago maritima* L. was investigated. The part of this salt marsh in which these species occur, is situated near coastal outer dunes and, as a form of nature management, grazing is applied during the growing season (Beeftink 1975, Blom 1983). Both species can be found separately and together in this area, and they mostly occur together in the communities *Armerion maritimae* with species

INTERACTIONS BETWEEN ECOLOGICAL DISCIPLINES AND
THE METHODS IN EXPERIMENTAL PLANT ECOLOGY

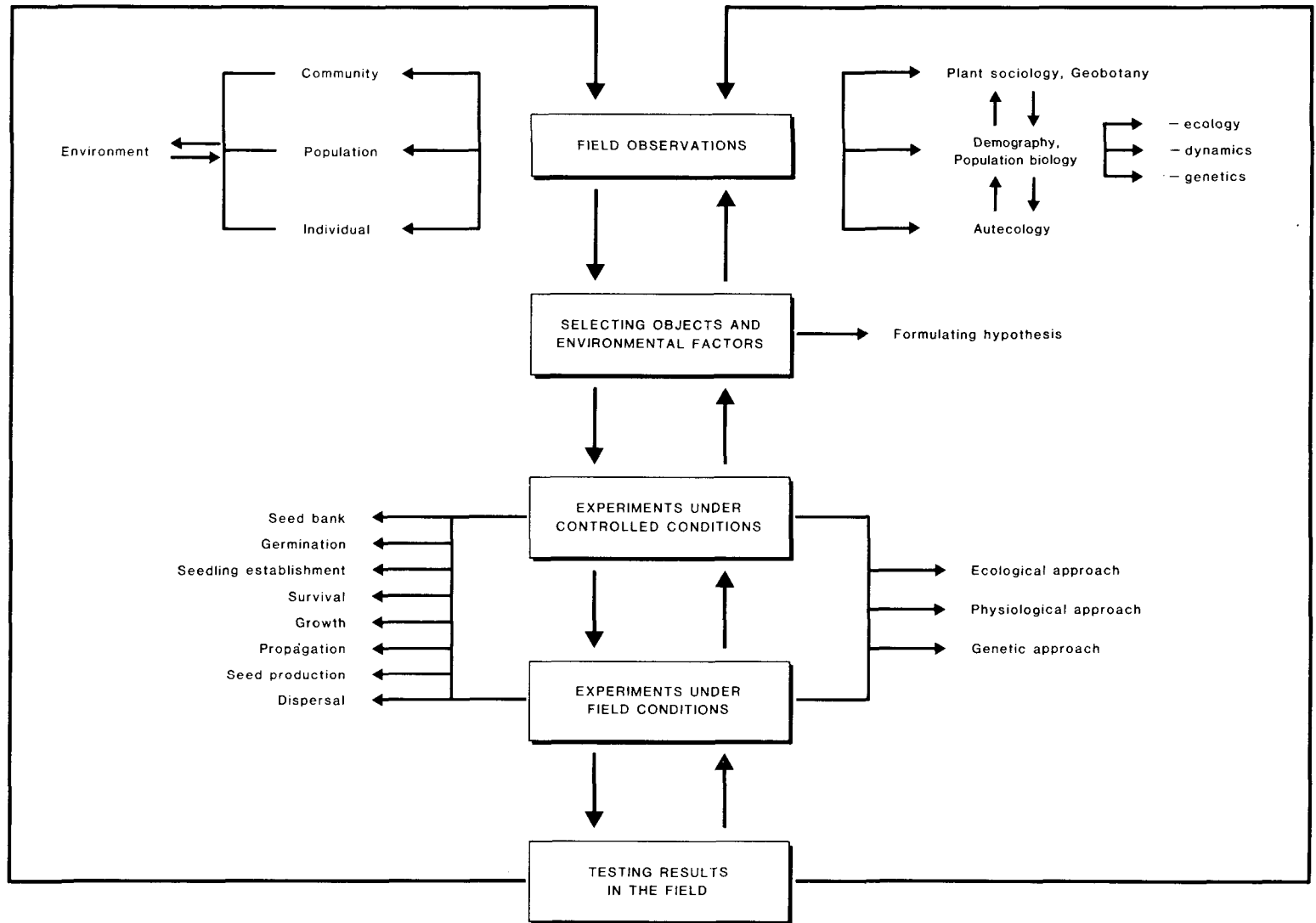


Fig. 1. Interactions between ecological disciplines and the methods in experimental plant ecology.

such as *Festuca rubra* L., *Juncus gerardii* Loisl., *Agrostis stolonifera* L., and *Artemisia maritima* L. and in Puccinellion maritimae with the species *Halimione portulacoides* (L.) Aellen, *Aster tripolium* L., *Limonium vulgare* Mill, and *Salicornia europaea* L. (Westhoff & den Held 1969). The first mentioned community is characterized by an intensive grazing regime. In the second community less grazing occurs, but, at these sites, flooding by seawater can be considered as the most important environmental factor.

In a previous study on the demography of *P. maritima* plants from seeds sown at four different sites at the 'Kwade Hoek' (Blom 1983) the impression was gained that changes in numbers of neighbouring *Plantago* and *Glaux* plants were in some way related to flooding regimes. At some regularly flooded sites, more *Plantago* than *Glaux* plants were found, but at other lower-lying sites the reverse conclusion must be drawn. From that study it was also known that flooding with seawater is an important cause of seedling mortality in *Plantago*. The seedlings of *Glaux* are more resistant. Jerling (1981) showed that the death of seedlings under these conditions must be partly ascribed to light deficiency. However, Cooper (1982) and Blom (1983), clearly demonstrated a relative high resistance of adult plants of *Plantago* to inundation with sea water. Rozema (1975) reported that regarding growth parameters *Glaux* seems to be adapted to moderately saline soils, but possibly salinity causes no stimulating influence on growth of this species.

To obtain an impression of the importance of regular flooding on the ratios of *Plantago* and *Glaux* a further field study was carried out in the summer of 1982. Both Armerion maritimae and Puccinellion maritimae communities were surveyed and fifty samples of 10 × 10 cm were randomly chosen within both vegetation types. In each sample the number of vegetative and generative rosettes and shoots of *Glaux* and *Plantago* was counted. The rosette diameter, shoot length, and distance between individual plants of both species were measured. In the Armerion community the mean densities per 10 cm² were 25.6 and 10.2 for *Glaux* and *Plantago*, respectively. In the Puccinellion community these values for both species were 22.1 and 8.6 plants, respectively. Between both communities these differences in

densities of the species were not significant. However, significant differences between both communities were found in the flowering capacity of the species under study (Blom & Bloot in prep.). In the Armerion community more flowering plants of both species were observed than in the Puccinellion community. It was remarkable that in both species, changes in ratios of plant numbers and plant characteristics were found between different growing seasons. Furthermore, these changes differed at different sites in the field and can be caused by abiotic environmental factors or by inter- or intraspecific interactions between both species.

As already suggested in the introduction to this paper, in the field situation it is nearly impossible to detect plant to plant interactions in relation to environmental factors. From observations in the field the hypothesis was postulated that in these parts of the area, species ratios have been influenced more through different flooding intensities than through changing grazing activities. This supposition was made as a starting-point for experimental investigations in the greenhouse. The main aim of these experiments was to answer the question of which way different seawater-flooding regimes will influence the densities of those plants. Furthermore the relationships between salinity of the environment, species ratios and growth responses of individual plants were studied. It is remarkable that only a few studies in which the effects of salinity on plants are combined with studies on the effects of plant to plant interactions are known from literature (Vince and Snow 1984). One of the few examples is the work of Goldsmith (1973) who published the results of competition experiments between two salt-marsh species. *Festuca rubra* suppresses *Armeria maritima* in mixtures watered with fresh water whereas contrasting results were found in mixtures watered with sea water, although growth of both species was much reduced. Another example is the recent work of A. Beeftink (1985), who studied the co-occurrence of *Plantago maritima* and *Limonium vulgare* in relation to flooding frequency and substrate. He found that the growth of *Plantago* was more reduced than that of *Limonium* at higher soil salinities. In outdoor and greenhouse experiments Groenendijk *et al.* (1987) studied the effects of different frequencies and times of in-

undation with sea water on monocultures and mixtures of five salt marsh-species.

Based on the observations on distances between individual plants in the field, all experiments started with inter-plant distances of 1.5 cm. Three species ratios were used: a pure culture of *G. maritima* and of *P. maritima* as well as a mixed culture with equal numbers of both species. Three treatments were applied: pots were watered with seawater diluted 1:2 and 1:4, respectively. In a third treatment, serving as a control, fresh water was used. The salt treatments started four weeks after potting up young even-aged seedlings. From that time each series of the pure and mixed cultures received every other day the fresh or appropriately diluted seawater by means of capillary rise. On alternate days, each pot was watered

on top with fresh water to prevent accumulation of salt in the topsoil. All these treatments lasted ten weeks.

The mortality of both species in pure and mixed cultures is presented in Fig. 2. From these results it is evident that *Glaux* is more sensitive to salinity than *Plantago*. Even at a 25% concentration *Glaux* plants succumbed in the pure culture by the third week of this experiment, whereas at this concentration no plants of *Plantago* were dead at the end of the experimental period. Furthermore, no plants of *Glaux* had survived the 50% treatment after eight weeks. More than 85% of the *Plantago* plants survived this treatment in the pure culture. Remarkable results were obtained in the mixed cultures. When these two species are growing together, *Plantago* appeared

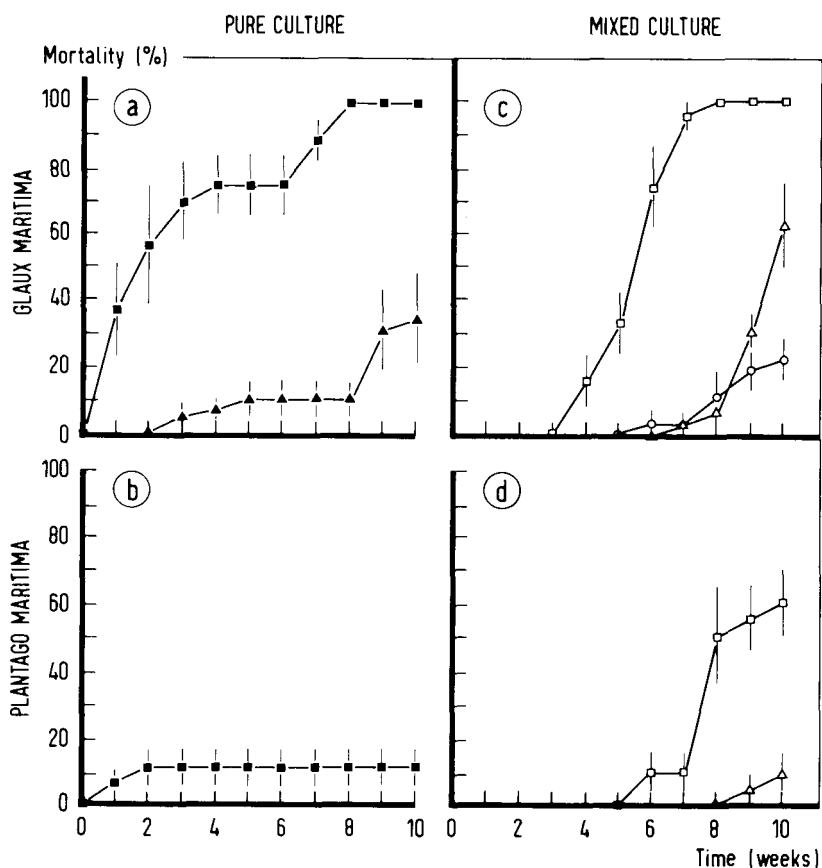


Fig. 2. Mean mortality of *Glaux maritima* and *Plantago maritima* in pure and mixed cultures under different salt treatments.

dot: demineralized water
 triangle: 25% seawater
 square: 50% seawater
 line: 2 × SE

to be the more competitive species. As far as survival concerned still more surprising was the observation that compared with the monocultures salt tolerance of both species seems to increase when growing together; a delayed but higher mortality was found. Probably the higher values in dead plants must be ascribed to interspecific density effects.

Fig. 3 gives the biomass development in all treatments. In the pure cultures lowest values were

obtained at the highest concentration of seawater, the differences in biomass development between the three treatments were the smallest in *Plantago*. *Glaux* plants showed highest biomass values in the fresh-water treatments of the monocultures. During the first weeks of the treatments the increase in biomass per plant in the 50% sea water treatment was very low. The only significant increase in biomass in the mixed cultures was found for *Plantago* under non-saline conditions.

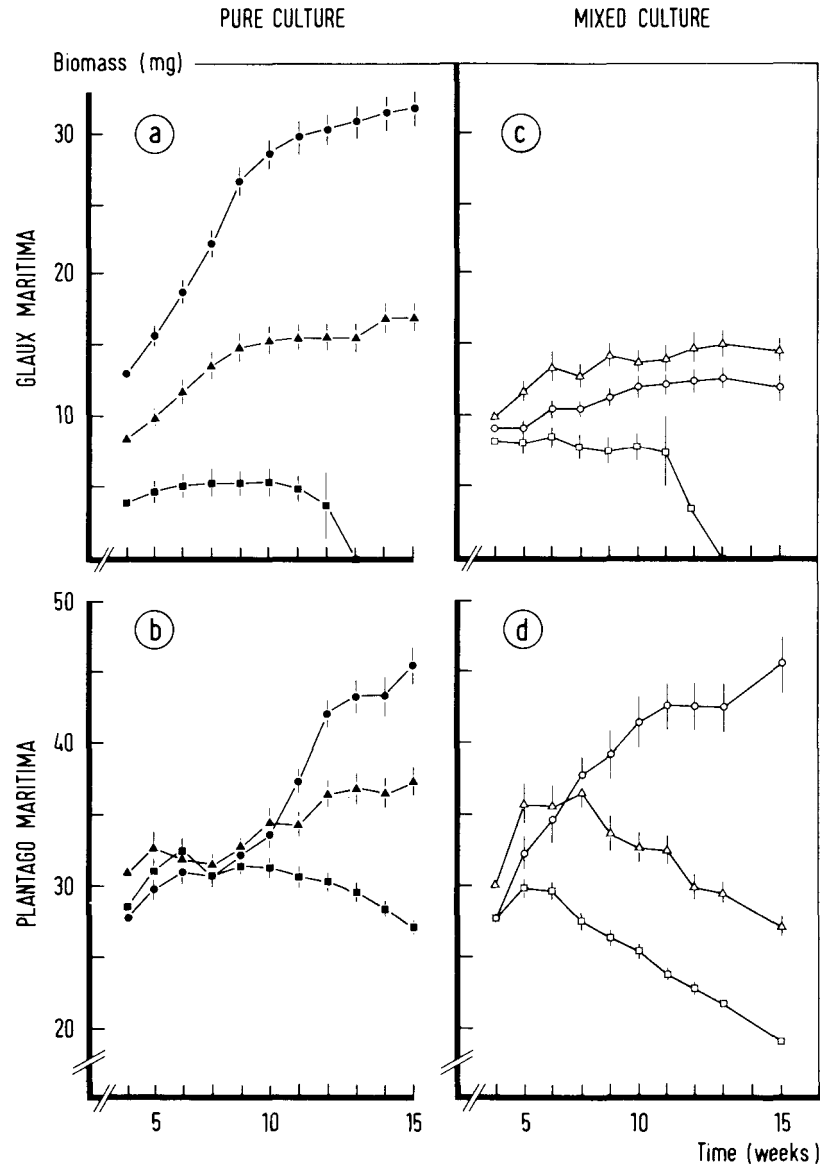


Fig. 3. Development of estimated shoot biomass per plant of *Glaux maritima* and *Plantago maritima* in pure and mixed cultures under different salt treatments. Symbols see Fig. 2.

In the fresh water and 25% treatment biomass production of *Glaux* was lower in mixed than in monocultures. In the controls of the mixed and monocultures *Plantago* produced the same biomass per plant. Both salt treatments showed a decreased biomass in mixed cultures.

In conclusion it can be stated that the results of these experiments strongly suggest that the co-occurrence in the field of *P. maritima* and *G. maritima* depends on the ratios between individual plants as well as on frequencies of seawater floodings. Re-checking of these results in the field indeed showed that seedlings of both species are very vulnerable to flooding, but the seedlings of *Glaux* are more resistant than those of *Plantago* (Blom & Bloot in prep.). For full-grown plants the opposite was observed when both species occurred together and interspecific competition may be expected. These observations strongly underline the fact that reactions of plants on changing environmental factors may differ at different stages in their life cycle. Furthermore research at the ecophysiological level is necessary to explain the observed differences in responses of plants growing in mixed or mono-cultures. Nevertheless, to a certain degree this study has clarified the mosaic pattern in co-occurrence of both species in relation to different levels of salinity in the field. At sites most frequently flooded in the late spring, seedlings of *Plantago* will be crowded out by *Glaux* seedlings. At sites, most frequently flooded in the summer period *Plantago* is the stronger competitor. In a study on the relationships between the position of different species in the salt marsh zonation and growth rates, Rozema *et al.* (1985) found that flooding with seawater significantly reduced the growth of *Plantago*; *Glaux* was less negatively affected by this factor. However, on the basis of studies by Blom (1983) differences in responses of *Plantago maritima* may be expected in different populations. Therefore further studies on the population level are necessary.

3. Demography of *Plantago major* ssp. *pleiosperma* in coastal areas

This study was initiated as a part of a multidisciplinary project on the relationship between

demographic, physiological and genetic properties of grassland species and the characteristics of their environment (van der Aart 1985). The aim of that project was to obtain an idea of the functioning of plant species in different habitats. Therefore this project was focussed on taxonomically closely related species in different environments. In such environments these species may have similar characteristics which can be ascribed to the genetic similarity of those species. When the closely related species occur in the same habitat, the differences in characteristics between those species may be attributed to local environmental conditions. For this project, carried out in the Netherlands, the genus *Plantago* was chosen because of the presence of five species within that genus, the distribution patterns, common appearance, co-occurrence of these species in different combinations, and the already proved experimental handiness (Blom 1979). The five species under study are *P. major* L., *P. media* L., *P. maritima* L., *P. lanceolata* L., and *P. coronopus* L. In order to understand the population biology of these species, demographic studies were combined with an experimental approach. For example, van Groenendael (1985, 1986) studied the life history of two populations of *P. lanceolata* from two different habitats using standard demographic techniques. In an open dune grassland with poor dry sandy soil and grazed during the growing season, he found small flat rosettes with many leaves and side rosettes.

The plants were able to flower in their second season and were short-living. The other habitat was a closed meadow, mown once a year in the early summer, and with a waterlogged soil rich in organic matter. The *Plantago* population in this habitat formed only few tall, erect leaves and no side rosettes. The plants were long-living and first flowering took place after several seasons.

In the wet meadow juvenile plants carry the greatest risk with highest mortality in winter. In the dry dune grasslands juveniles and adults share the risks more or less equally. The estimated half-life for juveniles in the wet and dry habitat was about four and eighteen months, respectively. In the wet meadow adults have an estimated half-life of about forty-nine months, whereas this value in the dune grassland is twenty months. Size-dependent survival of rosettes shows the same tendency

as age-dependent survival. The small rosettes carry the risks in the wet site but in the dry site these risks are equally shared between small and large plants.

Another example is a study on the demography of three coastal populations of *P. major* ssp. *pleiosperma*. At three sites, Groene Strand, Oostvoornse Meer, and Kwade Hoek, individual plants were followed during four years by making colour photographs of permanent plots (plot size: 0.25 m × 0.50 m).

The study sites, Groene Strand and Oostvoornse Meer, are adjacently situated on the Island of Voorne (the Netherlands) at a former beach embanked in 1965. In winter Oostvoornse Meer is frequently inundated by rain water; the soil at Groene Strand is better drained. The substrate of Oostvoornse Meer plots is relatively low in total nitrogen and total phosphate (c. 115 g.m⁻² and c. 42 g.m⁻², analysed after Troelstra *et al.* 1981). Other soil characteristics are: pH—H₂O 8.3; organic matter 1.3%; Cl 1.1 Eq.m⁻². The vegetation is species rich and there is virtually no grazing. Higher plant cover is around 30% and the plants, mostly short-living perennials, are characterized by a low growth rate and a low biomass (mean shoot dry weight of fructiferous plants c. 0.07 g). Although the soil in Groene Strand plots is slightly richer in organic matter, N and P, and the productivity of the vegetation is higher, the differences in values of these characteristics between both sites are relatively small.

Values of a greater difference were found at Kwade Hoek, situated 15 km south of Oostvoornse Meer. This area is a salt meadow, extensively grazed by cattle and occasionally flooded by sea-water (see part 2 of this paper). The soil is rich in organic matter, total N and total P (26.4%, 710 g.m⁻², 73 g.m⁻², respectively), and the level of chloride is high (21.0 Eq.m⁻²) as compared with the other sites. The vegetation is dense and highly productive (mean shoot dry weight of fructiferous plants c. 0.56 g; for further details of vegetation composition see part 2 of this paper). On this site *P. major* ssp. *pleiosperma* has a perennial life form.

Twenty-two plots were followed during 1980 to 1983; six at Groene Strand (G) and Kwade Hoek (KH) each, and ten at Oostvoornse Meer (OM). In location OM two subpopulations were

distinguished; a higher-lying population (OM 1—5) and a lower-lying one (OM 6—10). The number of rosettes as well as the number of spikes per plot, and the number of leaves and the height of each plant were recorded about five times a year. In addition, seed production was determined at the end of the growing season. The approximate biomass was calculated from the above-mentioned growth characteristics, using the method described by Noë & Blom (1982). The results of one representative plot per site are presented. The approximate biomass per plot in four successive years is shown in Fig. 4; the number of rosettes per plot are given in Fig. 5. Until 1983 the plots at Groene Strand showed a small increase in number of rosettes per plot, which was especially due to the high establishment and low mortality. The maximum biomass in those plots was relatively stable during this period; individual plants were smaller in 1983 than in previous years. In general, a decrease in total number of plants was found in the plots situated at Kwade Hoek, which was caused by a poor establishment of new plants in 1981 and 1982 and by the death of older plants during 1982 and 1983. Therefore the approximated biomass of *P. major* ssp. *pleiosperma* plants per plot decreased until 1982. The remaining plants produced more biomass in 1983. On the dry sites at Oostvoornse Meer only small differences in the maximum number of rosettes were found, but due to low survival of emerged seedlings in 1983, the total number of plants fluctuated strongly during that year. In the high-lying parts of the OM area, the maximum biomass in 1983 attained the same level as that of 1982, but in the first two years a higher value was found; plants from 1982 and 1983 were smaller than plants from previous cohorts. In the low-lying parts of this former beach plain the dramatic fall in number and biomass production of 1982 continued in 1983. At the dry sites, interspecific competition is not very likely, but intraspecific interactions may occur on these plots. The decrease in numbers of *P. major* plants at Kwade Hoek until 1982 was probably due to the absence of open sites necessary for germination. Table I shows that a great variation exists between the plots as well as among the sites as far as spike formation is concerned. In the plots of Oostvoornse Meer obviously fewer seeds were pro-

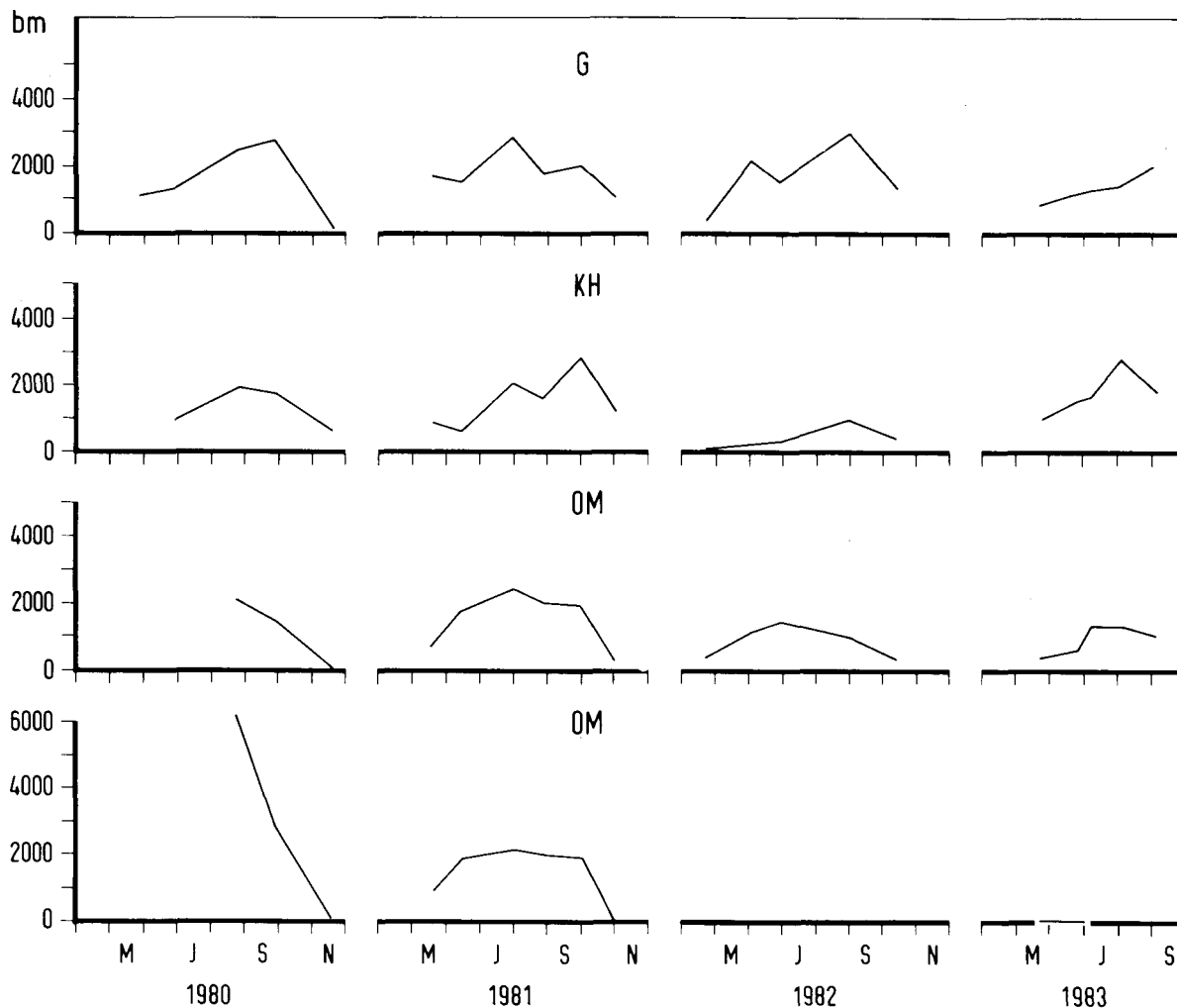


Fig. 4. The estimated biomass of *Plantago major* ssp. *pleiosperma* from 1980 to 1983 in plots on the island of Vooorne (G and OM) and on the island of Goeree (KH) in the Netherlands. The biomass (bm) is given in approximated values (length of longest leaf \times number of leaves per rosette) according to the method of Noë and Blom (1982). Upper OM graphs represent the higher-lying plots and lower OM graphs the lower-lying ones.

duced than in those of the other sites. Compared with the 1982 results the seed production of the Groene Strand plots reached the same level, whereas the Kwade Hoek and Oostvoornse Meer plots showed a definite decrease. Fig. 6 shows a corresponding linear relationship between the total number of seeds per plot and their dry weight. In conclusion it can be stated that populations of *P. major* ssp. *pleiosperma* are fairly stable at Groene Strand and Kwade Hoek. Oostvoornse Meer, however, is a site where changes in composition of the vegetation may take place within a few years, possibly as a result of environmental

changes. It is hypothesised that the present rapid expansion of *Glaux maritima* may be the cause of the disappearance of *Plantago major* ssp. *pleiosperma*.

From demographic data it is impossible to explain observed variation in survival distributions, growth rates or generative development in terms of physiological plasticity or genetic differentiation. Therefore experiments are essential in order to get a deeper understanding of these processes. In the field, reciprocal transplantation of ecotypes has been strongly recommended (e.g. Antonovics and Primack 1982) because it allows

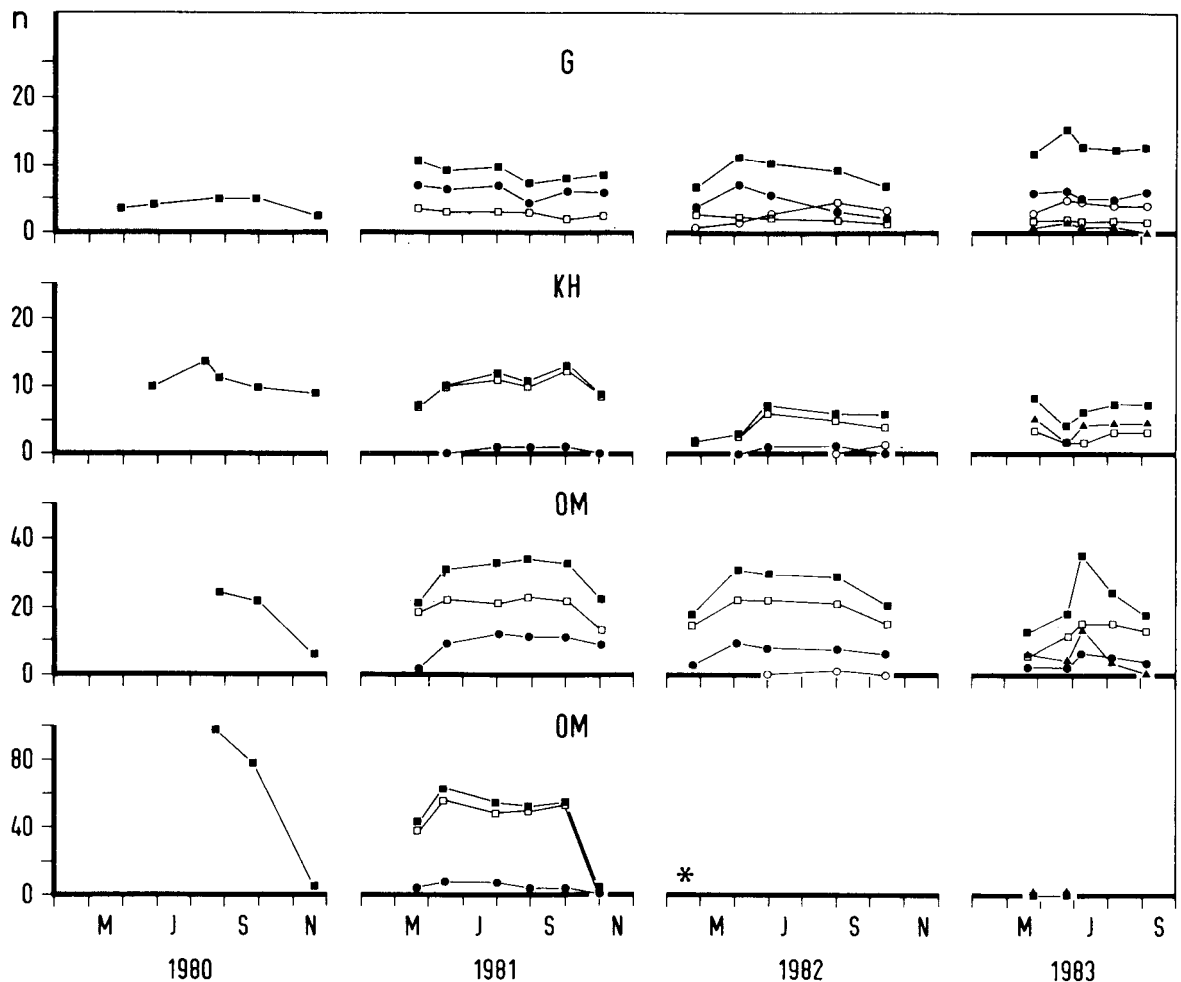


Fig. 5. The number of rosettes (n) of *Plantago major* ssp. *pleiosperma* from 1980 to 1983 in plots on Vorne and Goeree.

solid squares: total number of rosettes
 open squares: cohort of 1980
 solid dots: cohort established in 1981
 open dots: cohort established in 1982
 triangle: cohort established in 1983

direct comparison of different life histories in terms of fitness by recording fitness parameters such as survival. Van Groenendael (1985) studied the survival of seeds in the soil, germination, seedling establishment and survival of young adults in transplantation experiments with *Plantago lanceolata*. The demographic data on *Plantago major* ssp. *pleiosperma* and the knowledge that this species is a self-compatible wind pollinator with a high self-fertilization rate suggest strongly that genetic variation within populations is low. Furthermore, given the evidence of phenotypic

plasticity for some characteristics of *Plantago major* ssp. *pleiosperma* in water culture (Kuiper 1983), Lotz and Blom (1986) tested the hypothesis that differences in growth rate and generative development between the populations of this species are mainly determined by environmental factors. Therefore two experiments have been performed. Plants raised from seeds collected at three sites with different nutrient availabilities and interspecific interactions (Kwade Hoek, Oostvoornse Meer, and an inland river bank) were grown in a greenhouse at three nutrient levels. In

Table 1. Spikes and seed production in 1983 on plots (0.25 m × 0.50 m) at Groene Strand (G), Kwade Hoek (KH) and Oostvoornse Meer (OM) * disappearance of plot.

Plots	G 1	G 2	G 3	G 4	G 5	KH 1	KH 2	KH 3	KH 4	KH 6	KH 7
number of living plants	13	12	30	51	48	0	8	7	11	9	7
number of spikes	7	2	6	26	26	0	3	4	1	1	3
number of seeds	242	74	45	1036	608	0	334	225	185	115	225
total dry weight of seeds (mg)	54.6	16.5	10.6	168.0	107.7	0	69.1	55.7	41.6	26.1	38.2

plots	OM 1	OM 2	OM 3	OM 4	OM 5	OM 6	OM 7	OM 8	OM 9	OM 10
number of living plants	15	17	7	18	—	8	1	0	0	0
number of spikes	4	3	8	—*	3	1	0	0	0	0
number of seeds	94	48	61	—	27	19	0	0	0	0
total dry weight of seeds (mg)	20.0	9.1	12.6	—	4.9	3.5	0	0	0	0

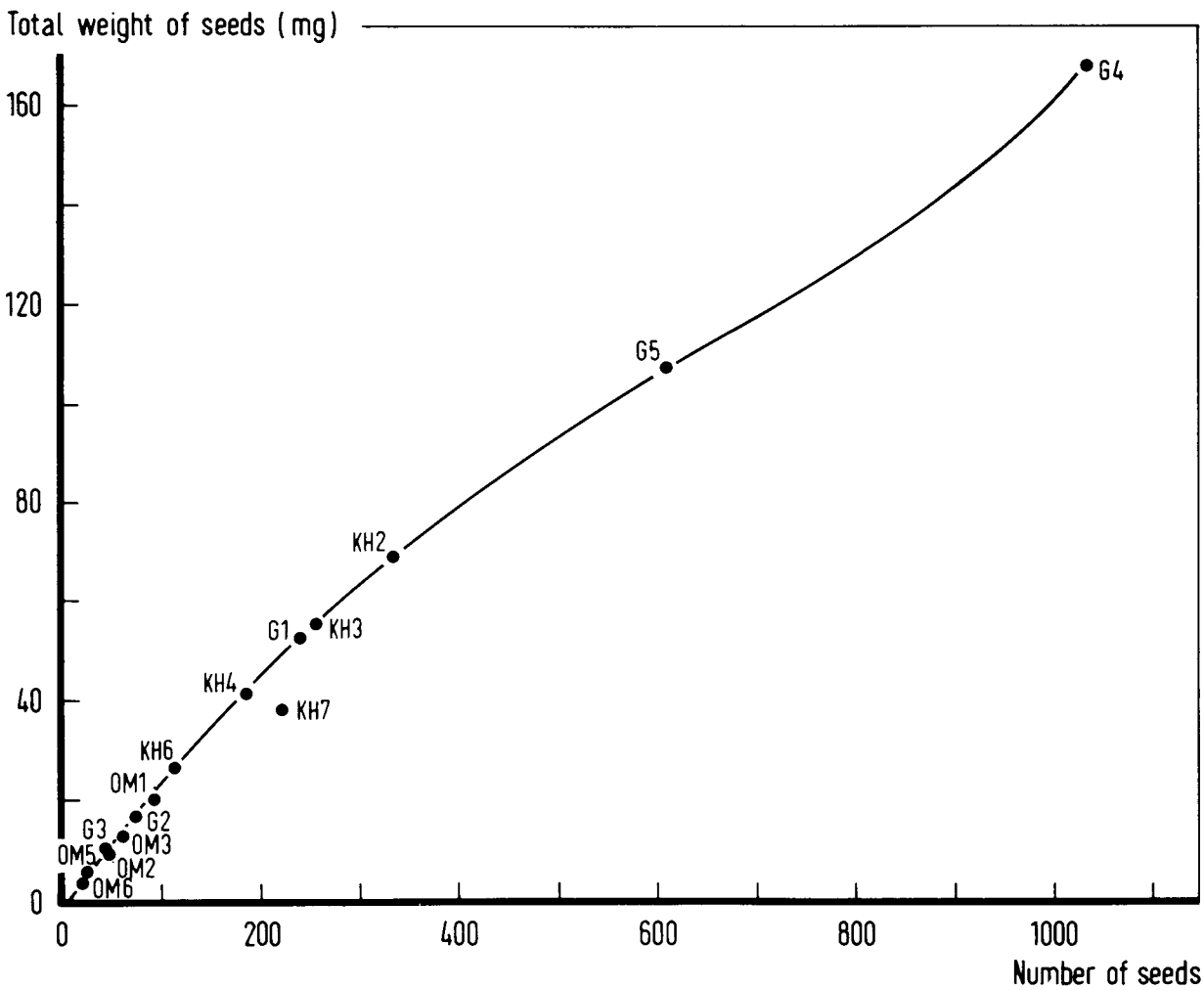


Fig. 6. Relationship between total seed dry weight and total seed number of *Plantago major* ssp. *pleiosperma* occurring on five plots at Groene Strand (G), six plots at Oostvoornse Meer (OM), and five plots at Kwade Hoek (KH) in 1983.

addition a reciprocal transplant experiment was carried out. Results of both experiments proved that vegetative and generative development were strongly affected by the supply of nutrients and thus depended on the study site. Nevertheless the results also indicated differences in plasticity between populations. Further studies suggested strongly that the populations are genetically differentiated in some life-history traits. Indications were obtained of the adaptive value of these differentiations because of apparent advantages of some home populations.

Further field and experimental studies on variation within and between populations as well as on the occurrence of *Plantago* plants in their communities and in relation to their abiotic environments are in progress.

4. Concluding remarks

These studies on the interactions between *Glaux maritima* and *Plantago maritima* as well as on the demography of *Plantago major* ssp. *pleiosperma* provide examples of experimental plant ecology. The basis of these studies was a survey in a salt marsh to determine what species are present, in what quantities and how are they distributed. Then knowledge was obtained on the communities they formed. Patterns and processes between species were studied. Attention was focussed on the relationships between some species and environmental factors. Efforts were made to answer questions such as: "How do these organisms interact with each other and with their environment as a resource-processing system?". Part of this problem was translated into a hypothesis and the design of experiments. Results were checked in the field. Nevertheless, generalizations on the occurrence of both *Plantago* species and *Glaux* may not be drawn from this study. One of the many remaining questions is: "Are there differences in reactions of those species from different populations". Furthermore, the complexity of biological systems needs alternative hypotheses and new experiments.

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